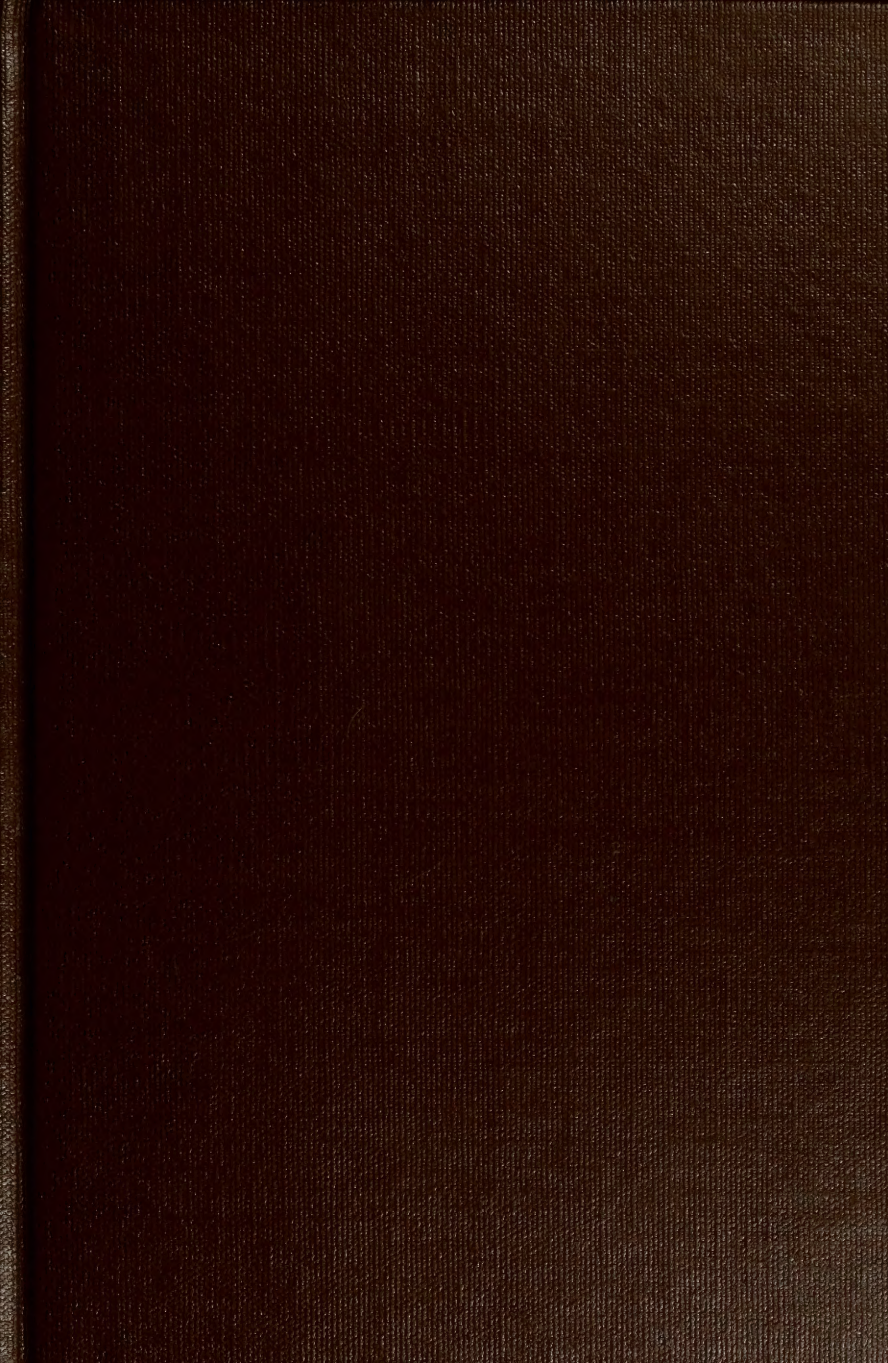






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**The Effects of Supplemental
Feeding and Fall Drawdowns
on the Largemouth Bass and
Bluegills at Ridge Lake, Illinois**

**George W. Bennett
Wickliffe Adkins
William F. Childers**

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This report is printed by authority of the State of Illinois, IRS Ch. 127, Par. 58.12. It is a contribution from the Section of Aquatic Biology of the Illinois Natural History Survey.

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The Effects of Supplemental Feeding and Fall Drawdowns on the Largemouth Bass and Bluegills at Ridge Lake, Illinois

George W. Bennett

H. Wickliffe Adkins

William F. Childers

IN 1963 WHEN THE PROGRAM described here was begun, studies of the fish population of Ridge Lake had been going on for 21 years (Bennett 1954a and 1954b; Bennett & Durham 1951; Durham & Bennett 1949 and 1951; Bennett, Adkins, & Childers 1969). These studies involved annual controlled public fishing during June, July, and August and draining censuses (usually in the spring) to gain estimates of the total population of fishes in the lake. Between these draining censuses we applied several types of primary or secondary population manipulation, or none at all, to explore the effects of these manipulations upon the fish populations and the yields of fishes. This period included 10 years of biennial draining of the lake and culling of small fishes; 5 years of fall drawdowns of the lake, with one draining census after 2 years and one after 3; 4 years of stable water levels and no manipulation of the fish population; and 3 years of testing the value of hybrid sunfishes for angling (Childers 1967:189). In the period 1941–1970, Ridge Lake has been completely drained and the fishes have been censused 10 times: in 1943, 1945, 1947, 1949, 1951, 1953, 1956, 1959 (in the fall), 1963, and 1970. On the basis of complete creel censuses in all years (except 1942, when the lake was closed to fishing) we were able to measure with some degree of certainty the type of fish population the lake would support and the effects of various management efforts on that population.

The fishes included in this investigation were largemouth bass, *Micropterus*

salmoides (Lacépède); bluegills, *Lepomis macrochirus* Rafinesque; warmouths, *Lepomis gulosus* (Cuvier); lake chubsuckers, *Erimyzon sucetta* (Lacépède); and channel catfish, *Ictalurus punctatus* (Rafinesque). Any other fishes that gained entrance to the lake through fishermen's minnow buckets or from the drainage basin were removed during the draining censuses. All of the fishes in the Ridge Lake population descended from 435 largemouth bass stocked in 1941, 129 bluegills stocked in 1944, 138 warmouths stocked in 1949, 558 lake chubsuckers stocked in 1960, and several groups of 6- to 12-inch channel catfish stocked in 1951, 1952, 1957, and 1969. The several stockings of catfish were necessary because channel catfish usually cannot reproduce successfully in Ridge Lake. All of the other fishes (bass, bluegills, warmouths, and chubsuckers) have maintained adequate populations through natural reproduction and survival with no stocking but the original one.

Experimental drawdowns were begun at Ridge Lake in 1951. In the spring of that year the lake was drained; the fishes were censused; and selected numbers of largemouth bass, bluegills, and warmouths were returned to the partially filled basin. The lake refilled before June 1 and was opened to controlled public fishing during the summer until September 1. Fishing was then terminated and the lake level was lowered 4.6 meters (15 feet), reducing the surface area from 6.9 to 2.0 ha (17 to 5 acres) and the maximum depth from 7.6 meters to 3 meters (25 to 10

Frontispiece.—A 3-meter (10-foot) drawdown at Ridge Lake. About one-third of the lake bottom, mostly in the upper end of the impoundment, is exposed by such a drawdown.

feet) without allowing any fishes to escape with the water. Thus, the fish population that had developed through natural reproduction and growth to fill a volume of water represented by a surface area of 6.9 ha¹ (17 acres) became concentrated in a volume represented by 2 ha (5 acres), a minor fraction of the full lake.

In 1952, after the lake had been open to public fishing during the summer, the lake level was again drawn down 4.6 meters (15 feet) in early September. In late March of 1953 the lake was completely drained, the fish were censused, and selected individuals were returned to the lake. These studies were reported in several papers (Bennett 1954a and 1954b; Bennett et al. 1969). The effect of the 4.6-meter drawdowns in 1951 and 1952 upon the bluegills was severe, reducing their numbers to the point that fewer small bluegills survived than did large ones. To insure the survival of enough bluegills to maintain successive year classes for fishing, it was decided to limit drawdowns to 3 meters (10 feet), leaving a maximum lake depth of 4.6 meters (15 feet) near the dam and a lake surface area of about 4.5 ha (11 acres). This procedure was followed in early September of 1953, 1954, and 1955, and the lake was drained again in the spring of 1956 and a census was made of the fishes. The lesser drawdowns of 1953–1955, inclusive, allowed the survival of a greater number of bluegills (both larger and smaller than 150 mm, or 6 inches, the length at which this fish was considered useful) than the 4.6-meter drawdowns allowed.

Following the spring lake draining and fish census of 1956, selected bass, bluegills, warmouths, and a few channel catfish were returned to the lake; the basin refilled by May. From March 1956 until October 1959 the water level in Ridge Lake was allowed to fluctuate around the crest of the tower spillway, i.e., without any drawdowns and with only minor fluctuations caused by runoff from rains in

the lake watershed. In October 1959, after four growing seasons for fishes, the lake was again drained completely and the fishes were censused. As in the years of the drawdowns, the lake was open to controlled public fishing during the summers of 1956–1959.

Thus, as a background for the experiment reported here, the authors had information on anglers' catches and total fish populations from 10 years of biennial draining of the lake and culling of the fishes, 5 years of drawdowns, and 4 years of stable water levels (including that part of 1959 important for fish reproduction and growth). From the lengths, weights, and scales of individual fishes taken by fishermen in 1951–1959 and from similar data gathered from fishes during the draining censuses of 1953, 1956, and 1959, it was possible to compare the growth rates of bluegills and their relative plumpness (condition) under a program of annual fall drawdowns and under another of stable water levels.

In the fish censuses of 1953 and 1956, many of the bluegills were of exceptional sizes but appeared to be comparatively thin. The supplemental feeding proposed at the beginning of the experiment reported on here was in part related to this observation.

Our laboratory production and culture of hybrid sunfishes (Childers 1967) had demonstrated that most species of sunfishes (Centrarchidae) quickly learn to feed upon commercial trout food if the pellets are small enough for them to swallow. Bluegills in laboratory aquaria became plump and grew rapidly on a trout pellet diet. If bluegills in Ridge Lake could be trained to eat fish food pellets to supplement their diet of natural foods, this additional food supply should be reflected in improved bluegill growth and condition. We wished to discover whether enough improvement in bluegill yield would occur to make artificial feeding practical. In 1963 following the spring fish census, we decided to combine September drawdowns of Ridge Lake (for the control of bluegill numbers) with supplemental feeding to increase the

¹Ridge Lake originally had a surface area of 7.3 ha (18 acres); silt deposits in the upper lake had reduced the area to about 6.9 ha by 1953 and to 6.5 ha by 1963.

growth rate, condition, and yield of these fish. Results would determine whether such a program was practical.

ACKNOWLEDGMENTS

Mr. H. Wickliffe Adkins, stationed at the Ridge Lake Laboratory during the summer months, supervised the fishermen and recorded their catches, fed the fishes twice daily, made daily observations on schools of bass fry and on the nesting of bluegills, assisted in age and growth analyses from fish scales, and recorded many biological happenings of importance to this study. Dr. William F. Childers planned and supervised the draining censuses in 1963 and 1970. Many people assisted in the fish censuses; these included Mr. Robert O. Ellis, Mr. Howard Crum (deceased), Mr. Robert T. Crompton, Mr. Dennis Dooley, Dr. D. Homer Buck, Mr. Richard Baur, Mr. Russell Rose, Dr. R. Weldon Larimore, Mr. H. W. Adkins, Mr. Ronald Havelka, Mr. David Mower, Mr. Edward Doyle, and Dr. George Sprungel, Jr., of the Illinois Natural History Survey staff; Mr. Alvin C. Lopinot, Mr. Arnold Fritz, and Mr. Rudy Stinauer of the Illinois Department of Conservation; and Dr. Leonard Durham and Scott Buck and other students from Eastern Illinois University. The manuscript of this paper was read and criticized by Dr. Horace W. Norton, Professor of Statistical Design and Analysis, Department of Animal Science, University of Illinois, and it was edited by Mr. Robert M. Zewadski of the Natural History Survey.

THE 1963 RESTOCKING OF RIDGE LAKE

Following the draining census of April 8-13, 1963, Ridge Lake was restocked with 2,270 small bass and 116 large ones, 4,492 bluegills, 1,335 warmouths, 1,020 lake chubsuckers, and 11 large channel catfish, a total of 9,244 fishes weighing 510.6 kg (1,125.5 pounds) (Table 1). The weight of these fishes was 78.8 kg per hectare, or 70.3 pounds per acre. Before the restocking, the lake contained 287 kg per hectare (256 pounds per

acre), almost four times the weight of fish returned to the lake.

A total of 1,000 channel catfish were stocked on May 21 and 29, 1969. These were Age III fish with an average total length of 259 mm (10.2 inches) and an average weight of 127 grams (0.28 pound); their total weight was 127 kg (280 pounds). On October 20 and 21, after the 1969 growing season was nearly over, an additional 1,000 channel catfish were released. These were also Age III fish, averaging 234 mm (9.2 inches) in total length and 113 grams (0.25 pound) and having a total weight of about 113.4 kg (250 pounds). All of these catfish originated in Arkansas in 1968 and were held in ponds on the Sam A. Parr Cooperative Fisheries Research Center in Marion County, Ill., until stocked in 1969.

After the spring draining and restocking of 1963, the fish population was fished by the public during the summers of 1963 and 1964 under the regular creel census system. Otherwise, the restocked fish population of Ridge Lake was allowed to expand for almost 2 years before any experimental management program was applied. During the summer of 1963 fishermen caught 299 largemouth bass, 358 bluegills, 49 warmouths, and 11 hybrid sunfishes, weighing a total of 113.4 kg (250 pounds) in 1,816 hours; the catch in 1964 was composed of 554 bass, 1,287 bluegills, 108 warmouths, and 65 miscellaneous hybrid sunfishes, weighing a total of 232.2 kg (512 pounds) in 2,346 hours of fishing. While the total yield per hectare in 1964 was twice that of 1963 (1963, 17.5 kg per hectare, or 15.6 pounds per acre; 1964, 35.9 kg per hectare, or 32 pounds per acre), both must be considered much below the average of the hook-and-line yields of fishes from Ridge Lake in the 1941-1963 period.

THE FEEDING PROGRAM

In May 1965, a supply of Splash Expanded Fish Food was purchased from the Ralph G. Wells Company of Monmouth, Ill. This food consisted of fish

Table 1.—Fishes returned to Ridge Lake following the draining census of April 8–13, 1963.

Species	Number	Weight in Kilograms	Weight in Pounds	Average Weight in Kilograms	Average Weight in Pounds	Percent of Total Weight	Total Weight	
							Kilograms Per Hectare	Pounds Per Acre
Largemouth bass								
1954-1955 year classes	8	24.1	53.1	3.01	6.64			
1956-1960 year classes	51	79.9	176.2	1.57	3.45			
Post-1960 year classes, large	57	57.0	125.6	1.00	2.20			
Post-1960 year classes, small	2,270	42.3	93.2	0.02	0.04			
Total	2,386	203.3	448.1			39.8	31.4	28.0
Bluegills								
146-216 mm	966	56.9	125.5	0.06	0.13			
76-145 mm	3,526	65.6	144.7	0.02	0.04			
Total	4,492	122.5	270.2			24.0	18.9	16.9
Warmouths								
146-216 mm	5	1.1	2.4	0.22	0.48			
76-145 mm	1,330	28.3	62.5	0.02	0.05			
Total	1,335	29.4	64.9			5.8	4.5	4.0
Channel catfish, large	11	44.8	98.8	4.07	8.98	8.8	7.0	6.2
Lake chubsuckers	1,020	110.5	243.5	0.11	0.24	21.6	17.0	15.2
Grand total	9,244	510.5	1,125.5			100.0	78.8	70.3

meal, corn distillers' dried solubles, meat and bone meal, soybean meal, cottonseed meal, wheat shorts, dehydrated alfalfa meal, brewers' dried yeast, yellow hominy feed, salt, vitamin A and D oils, vitamin A palmitate, D-activated plant sterol, d-alpha tocopherol acetate, thiamin hydrochloride, riboflavin supplement, calcium pantothenate, niacin, choline chloride, vitamin B-12, and trace amounts of nine additional compounds. The food was 32 percent protein and 4 percent fat. Total calories of energy per pound of finished feed were recorded as 1,884.

The original pellets were too large for most bluegills to swallow, but they soon learned to pick at the pellets until they could break off pieces small enough to swallow. After the first season, we purchased smaller pellets. About half of the

pellets would float for several hours. The rest would become waterlogged and sink almost at once.

Feeding was begun in late May or early June, and bluegill spawning beds were selected as feeding areas along with the area around the boat dock, where bluegills were observed to congregate (Fig. 1). The fishes were fed twice each day at 10:30 AM and 6:30 PM; the dry fish food pellets were broadcast by hand from a boat. The authors assumed that food pellets that sank into bluegill nests would be picked up by the guarding males for removal from the nests, at which time these fish would discover that the pellets were edible. This was exactly what happened, and bluegills were actively foraging for pellets after less than a week of daily feeding. In less than 2



Fig. 1.—H. W. "Wick" Adkins scattering food for bluegills from the laboratory pier.

weeks it became possible to distinguish bluegills that were eating pelleted food from those that were not by their obviously plump condition. Bluegills were more interested in the pellets that floated and those in the process of sinking than those that had reached the bottom. Probably most of the latter were picked up by catfish after dusk.

The quantity of pelleted fish food purchased and fed each season amounted to 1,360.5 kg in a 6.48-ha lake (1.5 tons per 16 acres of lake). This represented 210 kg per hectare per season (187.5 pounds per acre per season) or a little more than 2.2 kg per hectare per day (2 pounds per acre per day). The cost of the pelleted food used in this experiment was 6 cents per pound when purchased in lots of 1,000 pounds or more. With the feeding rate given above, the cost was \$11.25–\$12.19 per acre per season or \$27.80–\$30.12 per hectare per season. As mentioned above, feeding was begun in late May or early June, and it was continued through August.

It became evident that not all of the bluegills were feeding on the pelleted food, either because they had not learned to eat it or because they had not ranged into areas where the food was available. These fish appeared to be quite thin. Some fish appeared to be feeding almost exclusively on "Splash," and when we dissected them, we found that their digestive tracts were gorged with this food. These fish rather quickly became very plump and developed fatty deposits in the mesenteries between the loops of the intestine. After bluegills had fed exclusively on Splash for a month or more, the livers of these fish lost their dark red color and became pink, suggesting fatty degeneration.

FALL DRAWDOWNS

The early fall drawdowns proposed for Ridge Lake were similar in extent and timing to those performed there in the period 1951–1956. The objectives were: (i) to concentrate the fishes that had developed in a 6.5-ha lake (16 acres) with-

in a much smaller volume of water to cause selective mortality among the smaller fishes by stranding and by predation; (ii) to expose a significant portion of the lake bottom to oxidation and drying; (iii) to time the drawdown so that it would coincide with at least a month of warm weather during which water temperatures would remain at 18° C. (64° F.) or above. In the 1951–1956 period our draining censuses in 1953 and 1956 indicated that drawdowns within the range of 3.0–4.6 meters (10–15 feet) would reduce the number of bluegills in the Ridge Lake population by 80–90 percent.

Early fall drawdowns were conducted each year in early September, 1965–1969, inclusive. In 1965 the lake level was lowered 4.6 meters (15 feet) over a period of 15 days (August 30–September 13, inclusive). This slow drawdown was the result of some intermittent rains and our concern about the poor condition of the road beyond the boundary of the park, where the outlet channel from the lake became a ford for several farm families. By October 3, the water level was back up to within 3.4 meters (11 feet) of the full level.

In 1966 and 1967 the lake level was lowered 3 meters (10 feet) below the full level. In both years draining was started on August 28 and completed by August 31. The road ford was regaveled in 1966 so that automobiles could pass through a greater flow of water, and little or no fall precipitation occurred.

In the summer of 1968 there was visual evidence of an abundant supply of small bluegills. Consequently, in the fall of 1968 the lake level was again lowered by 4.6 meters (15 feet); in 1969 the drawdown lowered the lake level 4.3 meters (14 feet). The drawdown operation required 3 days in 1968 and 5 days in 1969.

In every year the lake had completely refilled by April. There was no evidence of loss of fish from winterkill, as even when the lake level was lowered by 4.6 meters (15 feet) there was always an area of water above the dam where the water was 3 meters or more in depth.

Table 2.—Total hook-and-line yield of fishes from Ridge Lake during 2 consecutive years following a draining census (with no supplemental feeding or drawdown), 1963–1964, and 5 consecutive years with summer feeding and early fall drawdowns, 1965–1969.

Year	Largemouth Bass			Bluegills			Warmouths			Channel Catfish			All Fishes		
	Kilograms Per Hectare	Pounds Per Acre		Kilograms Per Hectare	Pounds Per Acre		Kilograms Per Hectare	Pounds Per Acre		Kilograms Per Hectare	Pounds Per Acre		Kilograms Per Hectare	Pounds Per Acre	
1963	13.6	12.1		3.5	3.1		0.3	0.3		...	...		17.5 ^a	15.6 ^a	
1964	12.6	11.2		20.4	18.2		2.0	1.8		...	...		35.9 ^a	32.0 ^a	
<i>Average of 2 years without feeding and drawdowns</i>															
1965	13.1	11.6		12.0	10.6		1.2	1.0		0.0	0.0		26.7	23.8	
1966	19.4	17.3		53.8	48.0		7.7	6.9		0.2	0.2		81.2 ^a	72.4 ^a	
1967	18.6	16.6		83.9	74.8		3.1	2.8		2.4	2.1		108.0	96.3	
1968	17.8	15.9		89.8	80.1		2.3	2.1		1.2	1.1		111.2 ^a	99.2 ^a	
1969	20.3	18.1		64.2	57.3		3.4	3.0		0.4	0.4		88.3	78.8	
<i>Average of 5 years of feeding and drawdowns</i>	14.1	12.6		64.4	59.5		1.1	1.0		14.9	13.3		96.8	86.4	
	18.0	16.1		71.2	63.9		3.5	3.2		3.8	3.4		97.1	86.6	

^a Includes a few hybrid sunfishes and other miscellaneous fishes.

POPULATION DYNAMICS OF FISHES DURING THE FEEDING-DRAWDOWN PERIOD

Table 2 shows the yields of the four species of fishes taken by anglers in the fishing seasons 1963–1969, inclusive. This table also shows the averages of the yields for the 2 years when no supplemental feeding or drawdowns were conducted and for the 5 years of the feeding-drawdown program. From these averages it was obvious that a large difference occurred in the yield of bluegills, so large a difference that the average bluegill yield during the feeding-drawdown (f-d) period was about six times that for the pre-experimental 2 years. This difference occurred partly because the fish population was expanding in 1963–1964, and many of the bluegills were too small to interest anglers. This lack of interest in the small bluegills was further demonstrated by the light fishing pressure in those years (46 man-hours per hectare, or 114 man-hours per acre, in 1963; 56 man-hours per hectare, or 138 man-hours per acre, in 1964), as annual fishing pressures below 125 man-hours per hectare per season (309 man-hours per acre) indicated the poor quality of the fishing. However, the eight boats available for angling were seldom, if ever, used to the maximum during August in any year. Annual fishing effort, 1963–1969, is shown in Table 3.

Because the fish population was enumerated in total at the fish census and

restocking in 1963 (at the beginning of the experiment) and in the fish census in 1970 (at the end of the experiment) and because the fishermen's total catch was recorded each year, it was possible to show the population dynamics of each individual species during the 7-year period.

Largemouth Bass

Table 4 shows that the lake was restocked in the spring of 1963 with 2,270 bass of less than 254 mm (10 inches) and 116 that averaged more than 1.36 kg (3 pounds) each. No bass were available in the 254–305-mm (10–12-inch) range, a situation that is inexplicable. In the following 7-year period, the catch consisted of 2,984 bass of less than 254 mm (10 inches), 962 bass of 254–305 mm (10–12 inches), and only 91 larger than 305 mm (12 inches). The record shows that 59 bass ranging in weight from 1.4 to 3.6 kg (3.0–8.0 pounds) were returned to the lake in 1963 and that 22 bass averaging 2.4 kg (5.35 pounds) and 47 averaging 1.2 kg (2.65 pounds) were exposed in the 1970 census, 7 years later. Therefore, one must assume that Ridge Lake contained at least 10 bass weighing more than 2.25 kg (5 pounds) each and 40 or more additional bass, each weighing 1.1 kg (2.5 pounds) or more, through this period of years. In spite of this valid assumption, fishermen caught only 49 bass as large as 1.1 kg (2.5 pounds) and only 2 larger bass, each weighing between 2.7 and 3.2 kg (6 and 7 pounds). At the same time, they were catching and removing 2,984 bass smaller than 255 mm (10 inches) at rates between 300 and 600 per season (fishermen were asked to bring in all bass regardless of size, but we know that some did not).

In general, Ridge Lake bass populations subjected to annual drawdowns over a period of years were composed of many small bass, a small number of very large ones, and relatively few of intermediate sizes. The thinning effect of the fall drawdown reduced the predation pressure on bass eggs and fry in the following

Table 3.—Fishing effort, in man-hours per hectare and per acre, expended by fishermen during the seasons 1963–1969, inclusive, at Ridge Lake.

<i>Year</i>	<i>Man-Hours Per Hectare</i>	<i>Man-Hours Per Acre</i>
1963	46	114
1964	56	138
1965	98	242
1966	103	254
1967	107	265
1968	107	264
1969	102	252

Table 4.—Population dynamics of largemouth bass in Ridge Lake, 1963–1970, including the feeding-drawdown period (1965–1969).

Year	Smaller Than 254 mm (10 inches)			254–305 mm (10–12 inches)			Larger Than 305 mm		
	Num- ber	Weight in Kilograms	Average Weight in Grams	Num- ber	Weight in Kilograms	Average Weight in Grams	Num- ber	Weight in Kilograms	Average Weight in Grams
1963 restocking	2,270	42.3	18	...		...	116	161.0	1,388
<i>Anglers' catch</i>									
1963	91	3.9	43	...		...	70	76.9	1,098
1964	537	57.2	106	...		...	17	24.1	1,418
1965	466	52.6	113	235	73.2	311	..		
1966	605	68.9	114	128	51.5	402	..		
1967	307	41.0	134	260	69.2	266	3	4.8	1,600
1968	589	51.1	87	238	78.7	331	1	1.2	1,200
1969	389	40.8	105	101	50.4	499	..		
<i>Total catch</i>	2,984	315.5	...	962	323.0	...	91	107.0	
1970 census	2,146	69.2	32	167	43.3	259	107	132.1	1,234

spawning season, and successive strong year classes were produced, some of which were later reduced by predation from a preceding year class. This cycle of production created by the drawdown caused severe competition and slow growth among the small bass and rapid growth among the few that survived the food competition, stranding, and predation of their first season and the fishing pressure of their second season.

Severe predation upon small fishes other than bass was indicated by changes in the population of lake chubsuckers in the 7 years of this experiment. In 1963, 1,020 lake chubsuckers were restocked, totaling 110 kg (243 pounds) and averaging 108 grams (0.24 pound) each. Only 232 chubsuckers, weighing 44.7 kg (98.5 pounds) and averaging 193 grams (0.42 pound), appeared in the 1970 census.

These fish were too large to be preyed upon by any but the very largest bass and catfish; none smaller had managed to survive.

Bluegills

A total of 4,492 bluegills, mostly within the 100- to 140-mm (4- to 5.5-inch) length range were returned to Ridge Lake after the spring census of 1963 (Table 5). These bluegills constituted a population of 693 per hectare (281 per acre). With such a small population, very few were caught in 1963, but by 1964 enough bluegills were present to increase food competition and improve the catch. Large catches of bluegills exceeding 150 mm (6 inches) in total length were made in each year from 1965 to 1969, inclusive, or throughout the f-d period (Table 5 and Fig. 2), and quite large numbers of small



Fig. 2.—Fishermen returning to the laboratory pier with large catches of bluegills.

Table 5.—Population dynamics of bluegills in Ridge Lake, 1963–1970, including the feeding-drawdown period (1965–1969).

Year	Smaller Than 152 mm (6 inches)			152 mm or Larger		
	Num-ber	Weight in Kilograms	Average Weight in Grams	Num-ber	Weight in Kilograms	Average Weight in Grams
1963 restocking	3,526	65.6	18	966	56.9	59
Anglers' catch						
1963	272	15.2	56	86	7.5	87
1964	141	4.6	33	1,146	127.6	111
1965	977	53.9	55	2,282	294.5	129
1966	1,670	93.9	56	3,916	448.7	114
1967	509	27.2	53	4,007	554.0	138
1968	1,880	79.8	42	2,285	336.0	147
1969	2,126	100.2	47	2,754	331.7	120
Total catch	7,575	374.8	..	16,476	2,100.0	...
1970 census	7,967	306.2	38	1,579	197.5	125

bluegills were caught by fishermen in 1966, 1968, and 1969. Bluegills of desirable sizes averaged 127 grams (0.28 pound) each.

Of some interest is the fact that the fishing pressure was nearly the same during each of the f-d years (1965–1969, inclusive) (Table 3), in part a reflection of the goodness of the fishing.

When the lake was drained in April 1970, it contained about 9,500 bluegills larger than 75 mm (3 inches). Most of these fish were within the 100- to 140-mm (4.0- to 5.5-inch) length range; however,

about 1,600 were larger than 150 mm (6 inches), and many were more than 178 mm (7 inches).

In 7 years, fishermen had taken 16,476 large bluegills (Table 5) and 7,575 smaller ones. The large bluegills averaged 178 mm and 127 grams (7.0 inches and 0.28 pound) each; the small ones, 49 grams (0.11 pound).

Warmouths

More than 4,500 warmouths were taken in the 1963 draining, and most of them were less than 150 mm (6 inches) in

Table 6.—Population dynamics of warmouths in Ridge Lake, 1963–1970, including the feeding-drawdown period (1965–1969).

Year	Smaller Than 152 mm (6 inches)			152 mm or Larger		
	Num-ber	Weight in Kilograms	Average Weight in Grams	Num-ber	Weight in Kilograms	Average Weight in Grams
1963 restocking	1,330	28.3	21	5	1.1	220
Anglers' catch						
1963	49	2.4	49	...	...	...
1964	21	1.4	67	87	11.3	130
1965	211	15.8	75	279	34.0	122
1966	30	1.9	63	74	18.6	251
1967	8	0.4	50	110	14.9	135
1968	65	3.0	46	138	18.6	135
1969	34	1.8	53	44	5.7	130
Total catch	418	26.7	..	732	103.1	...
1970 census	422	21.9	52	134	17.5	130

length. Approximately 1,330 of the larger ones were restocked following the census (Table 6). The catch of both large and small warmouths was quite insignificant, 732 large warmouths and 418 small ones being brought in by fishermen in 7 years.

There were 556 warmouths in the census of April 1970, and only 134 of these were more than 150 mm (6 inches) in total length.

That the total number of warmouths was reduced during this period suggests that the drawdown was not obviously effective in stimulating an increase in the warmouth population. Warmouths have been observed to eat the pelleted food, and they presumably grow well on it. In 1966, for example, the 74 warmouths that comprised that part of the catch which exceeded 150 mm in total length averaged 251 grams (0.56 pound) each, or more than twice as much as the average weight of large bluegills caught in that year.

The warmouths, as is usually the case in Illinois (Larimore 1957:70), in competition with largemouth bass and bluegills in Ridge Lake, have contributed very little to the fish population and to the

anglers' yield in every phase of experimental fish management that has been tested, including the f-d program.

Channel Catfish

Eleven large channel catfish appeared in the census of 1963 and were returned to Ridge Lake (Table 7). These were all very large fish, averaging 4 kg each (8.9 pounds). No catfish was caught by fishermen until 1965 when two small fish weighing 172 grams each (0.38 pound) were taken. These were believed to represent survivals from a spawn produced in the lake in 1963. Others of this year class probably survived because some catfish were taken each year, 1966-1969, inclusive (Table 7). These catches probably represented this same year class, because their average size moved progressively upward with each successive season: 1966, 1 kg; 1967, 2.3 kg; 1968, 3 kg; 1969, 3.4 kg (2.3, 5.1, 6.6, 7.5 pounds).

It appears improbable that any of the 11 catfish returned to the lake in 1963 were caught. However, it is likely that the 32 large catfish caught by fishermen, 1966-1969, and the 22 large fish taken in the census of 1970 were all survivors from a year class of fish produced in

Table 7.—Population dynamics of channel catfish in Ridge Lake, 1963-1970, including the feeding-drawdown period (1965-1969). The large catfish restocked in 1963 apparently produced a few young in 1963 or 1964.

Year	Smaller Than 304 mm (12 inches)			304 mm or Larger		
	Num- ber	Weight in Kilograms	Average Weight in Kilograms	Num- ber	Weight in Kilograms	Average Weight in Kilograms
1963 restocking	...			11	44.8	4.07
Anglers' catch						
1963	...			..		
1964	...			..		
1965	2	0.3	0.15	..		
1966	...			15	15.4	1.03
1967	...			3	7.0	2.33
1968	...			1	3.0	3.00
1969	110 ^a	52.1	0.47	13	44.2	3.40
Total catch	112	52.4		32	69.6	
1970 census						
Offspring of						
1963 restocking	...			22	86.3	3.92
1969 stocking	805	90.9	0.11	650	428.8	0.66
Total	805	90.9	0.11	672	515.1	

^a 1,000 channel catfish 203-330 mm (8-13 inches) long were stocked in Ridge Lake on May 1, 1969 from the Sam A. Parr Fisheries Research Center, Marion County, Ill., and 1,000 more of the same size range were stocked on October 21 and 22, 1969 after the fishing and feeding season.

Ridge Lake, probably in 1963. These channel catfish were able to survive in 1963 because the fish population was well below the carrying capacity of the lake in that year, and predation pressure was probably low.

THE EFFECTS OF EARLY FALL DRAWDOWNS IN REDUCING BLUEGILL NUMBERS IN RIDGE LAKE

With stable water levels, the bluegill population of Ridge Lake increases rapidly in total number with each successive spawning season and with apparently little regard for the number of largemouth bass present. In 1949 and 1950 the bass population of Ridge Lake was exceptionally large, and no bluegills other than those that remained in pockets of the old stream channel during the 1949 census were left in the lake. Yet the population found in the 1951 census amounted to 51,963 bluegills larger than 65 mm (Table 8). The 66,600 bluegills that appeared in the 1947 census originated from 61 large bluegills returned to the lake following the 1945 census. If the period between censuses is longer than 2 years, the numbers of bluegills become larger. For example,

the 3-year period 1960–1962 started with zero bluegills and a dry lake basin over the winter of 1959–1960. A few bluegills appeared in 1960 from an unidentified source. These multiplied in competition with 4,500 hybrid sunfishes and a bass population that was building up to 6,000 small fishes. In 3 years the bluegills numbered 85,500.

Still larger numbers of bluegills were present after the four growing seasons with stable water levels, beginning in March 1956 and continuing until October 1959. After the 1956 census, 1,008 bluegills were restocked, and in the 1959 census the bluegill population was 92,700. It is impossible to suggest how much this population might increase numerically, but it seems apparent that in a relatively short period, say 7–10 years, the bluegills would become so dominant as to curtail the success of bass reproduction. Within the range of bluegill numbers (and time) shown in Table 8, there was no evidence of a reduction of bass numbers; in fact, the 6,200 bass exposed in the 1963 census, when 85,500 bluegills were present, was the largest population of small bass ever recorded for Ridge Lake.

The effects of the drawdowns on the

Table 8.—Total numbers and total weights in kilograms of fishes collected in several draining censuses at Ridge Lake when bluegills were present and when water levels were stable for two or more seasons prior to the census. Similar data are presented for censuses following 2–5 years of early fall drawdowns.

Year of Census	All Fishes		Largemouth Bass		Bluegills		Other Fishes	
	Num- ber	Weight in Kilograms	Num- ber	Weight in Kilograms	Num- ber	Weight in Kilograms	Num- ber	Weight in Kilograms
<i>Stable water</i>								
1947	69,801	2,092.5	2,509	257.0	66,629	1,577.8	663	257.7
1951	54,574	1,336.8	1,510	407.5	51,963	858.4	1,101	70.8
1959	97,312	1,906.0	2,354	240.0	92,669	1,246.5	2,289	419.4
1963	99,791	1,856.8	6,218	359.8	85,528	1,043.9	8,045	453.2
<i>Average</i>	<i>80,370</i>	<i>1,798.0</i>	<i>3,148</i>	<i>316.1</i>	<i>74,197</i>	<i>1,181.6</i>	<i>3,024</i>	<i>300.3</i>
<i>Fall drawdowns</i>								
1953 ^a	10,377	901.0	1,964	204.8	7,476	449.9	937	247.1
1956 ^b	20,308	1,538.7	2,242	289.3	17,180	924.6	886	324.8
1970 ^c	14,234	1,440.0	2,420	244.6	9,546	503.8	2,268	691.7
<i>Average</i>	<i>14,973</i>	<i>1,293.2</i>	<i>2,209</i>	<i>246.2</i>	<i>11,401</i>	<i>626.1</i>	<i>1,364</i>	<i>421.2</i>

^a Drawdowns of 4.6 meters (15 feet) in 1951 and 1952.

^b Drawdowns of 3.0 meters (10 feet) in 1953, 1954, and 1955.

^c Drawdowns varying between 3.0 and 4.6 meters (10 and 15 feet) in 1965, 1966, 1967, 1968, and 1969.

bluegill populations become evident when the bluegill numbers at the bottom of Table 8 are compared with those at the top. Also, a direct relationship apparently exists between the severity of the drawdown and the extent of bluegill population reduction, as indicated by the 1953 and 1956 census figures.

During a drawdown, small bluegills are more vulnerable to stranding and predation than are bluegills larger than a certain minimum size (25–100 mm). The larger fishes may live through several drawdowns, while relatively few of the small ones survive. The reduced population remaining in Ridge Lake after a drawdown (10,000–20,000 fishes instead of 50,000–100,000) becomes an expanding population in the refilled lake, with plenty of available food and space for reproduction and growth in the growing season following a fall drawdown.

Table 8 shows no large differences between the numbers of largemouth bass with and without drawdowns. Drawdowns are associated with successful reproduction of largemouth bass during the following spawning season, but when a drawdown is scheduled for every fall the young bass of each spawning season may be decimated by yearling bass from the previous year class. The discovery that drawdowns are almost always followed by successful bass fry production and the survival of these little fish beyond the size subject to predation by bluegills suggests a "surefire" method of producing a new year class of bass when a stunted bluegill population has been curtailing all bass reproduction. It is evident that annual drawdowns, with or without supplemental feeding, do not result in bass populations with superior potential for bass fishing although they probably should not be considered below average.

A COMPARISON OF THE EFFECTS OF VARIOUS MANAGEMENT TECHNIQUES ON ANGLING YIELDS

To make a comparison of management techniques, data from several fishing seasons directly affected by these techniques

were selected and averaged (Tables 9 and 10). For example, several years in the biennial draining-and-culling period, 1941–1951, were characterized by large catches of largemouth bass. The year 1948 was selected because of the alternate years in which the lake was not drained, it was the year of the largest catch of bass.

In the first period of drawdown studies, 1951–1956, catches for the years 1951 and 1953 were omitted because they followed spring censusing operations in which the lake was completely drained and selected fish were returned. These operations also affected all other aquatic biota. While the fish returned to the lake after the 1953 census must have been influenced by the drawdowns of the fall seasons of 1951 and 1952, the fish population returned was probably more a reflection of the draining and censusing operation than of the drawdowns. The draining operation of 1956 again upset the replacement fish population. It marked the beginning of the "steady-state" period which lasted from May 1956 to October 1959. Only the years 1957, 1958, and 1959 were used to represent this period of stable water levels.

In the f-d period the years 1965–1969 were included because, as mentioned previously, feeding was begun during the summer of 1965 and the first drawdown was made in the fall of 1965.

In Table 9, statistics are shown for a comparison of the yields of the four major species of fishes in Ridge Lake for the several periods mentioned above. The average yield of bass of 18 kg per hectare (16.1 pounds per acre) for the f-d period is lower than that of any of the other periods shown and was exceeded by nearly twice this average in 1948, one of the best bass fishing seasons.

It seems safe to assume that annual fall drawdowns at Ridge Lake did not result in the production of large numbers of desirable-sized bass. Bass fishing was considerably better in the period when we drained the lake every 2 years and removed bass smaller than 200–255 mm (8–10 inches) along with large numbers of smaller bluegills. Under this culling

Table 9.—Total or average hook-and-line yields from fishing in Ridge Lake during the feeding-drawdown and other periods: 1948, when the bass catch was exceptionally large; the average of yields for 1952, 1954, and 1955 after a season or more of early fall drawdowns without feeding; and the average of yields for 1957, 1958, and 1959 during the period of stable water levels.

Year(s)	Largemouth Bass		Bluegills		Warmouths		Channel Catfish		All Fishes	
	Kilograms Per Hectare	Pounds Per Acre	Kilograms Per Hectare	Pounds Per Acre	Kilograms Per Hectare	Pounds Per Acre	Kilograms Per Hectare	Pounds Per Acre	Kilograms Per Hectare	Pounds Per Acre
Good bass season, 1948	32.1	28.6	57.6	51.4	...	...	...	...	89.7	80.0
Drawdowns only; 1952, 1954,										
1955 average	22.3	19.9	41.0	36.6	3.7	3.3	10.1	9.0	77.2	68.9
Stable water; 1957, 1958,										
1959 average	20.5	18.3	58.7	52.4	5.6	5.0	7.8	7.0	92.7	82.7
Feeding and draw- downs; 1965-1969 average	18.0	16.1	71.6	63.9	3.6	3.2	3.8	3.4	97.1	86.6

Table 10.—Average number per unit of lake surface and average weight of largemouth bass and bluegills taken by anglers in 1948, a very successful year for bass fishing, and in years affected by drawdowns only, by stable water levels, and by supplemental feeding and drawdowns.

Year(s)	Largemouth Bass				Bluegills			
	Number Per Hectare	Average Weight in Grams	Number Per Acre	Average Weight in Pounds	Number Per Hectare	Average Weight in Grams	Number Per Acre	Average Weight in Pounds
Good bass season, 1948	89	361	36	0.79	801	72	324	0.16
Drawdowns only; 1952, 1954, 1955	163	137	66	0.30	416	98	168	0.22
Stable water; 1957, 1958, 1959	138	148	56	0.33	797	74	322	0.16
Feeding and drawdowns; 1965-1969	103	175	42	0.38	692	103	280	0.23

method, we selected for fast-growing bass and removed the slow-growing ones. This method also stimulated the production of large new year classes of bass at 2-year intervals.

It is also evident from the data in Table 9 that the f-d operation did not improve the catch of warmouths and channel catfish. This was due in part to the relatively small numbers of both species. We made no direct observations on whether warmouths were eating the pelleted food although they readily learned to eat it in the laboratory. Channel catfish fed well on "Splash," as was indicated in Table 7 by the large annual increases in the average weight of the catfish caught (except those stocked in 1969), 1966-1969, inclusive. However, so few were in the lake that their weight per hectare was small.

Table 10 shows average numbers of bass and bluegills caught per unit of lake surface and their average individual weight under the several methods of management. With both largemouth bass and bluegills, apparently a negative relationship exists between the average number of fish caught and their average size. If one may assume a positive relationship between the number of fishes available in any season and the number caught by anglers, one may also assume that, in years when the fish population is relatively small, each individual fish may have plenty of food available and therefore may grow rapidly and attain a large size. Thus, because the population is relatively small, each individual is subjected to little competition for food and space. If recruitment does not greatly increase the population, it is reasonable to assume that the average size of the individuals in this population will be large. Conversely, overproduction, the survival of new year classes, and the consequent competition for food and space will result in fishes of small average size. One can therefore assume a relationship between the catch of fishes and the average size of those fishes although so many variables are involved that the relationship may be quite obscured.

THE EFFECTS OF SUPPLEMENTAL FEEDING AND DRAWDOWNS ON THE CONDITION OF LARGEMOUTH BASS AND BLUEGILLS

We believed that the effects of supplemental feeding of the fishes of Ridge Lake would become evident through changes in the growth rate and in the relative plumpness of the fishes. The procedure of allowing two seasons to pass after the restocking of the lake before any experimental management or feeding was begun gave results from those 2 years that we could compare with results from 5 years of f-d operations. Also, results from the 5-year f-d period could be compared with results from previous Ridge Lake studies (Bennett 1954a; Bennett et al. 1969): 5 years of drawdowns without feeding, 10 years of biennial draining of the lake and culling of the fishes, and 4 years of stable water levels.

It is convenient to begin by comparing the condition of bass and bluegills collected in 1963 and 1964, when no supplemental feeding or drawdowns were conducted, with collections made in 1965–1969, inclusive, when the fish were fed daily during the summer and the lake level was dropped 3 or more meters each fall and held down as long as the weather was warm.

Fishermen's catches at Ridge Lake were measured as total lengths in tenths of inches and weights in hundredths of pounds. Therefore, it was convenient to use the *Index of Condition*, *C*, formulated by Thompson & Bennett (1939:16–17)

$$C = \frac{W}{L^3} 10,000$$

in which *W* is weight in pounds and *L* is length in inches.

To interpret results from this formula, one must know that bluegills showing an index of condition, *C*, of 6.0–7.0 are in poor flesh; those showing a condition of 7.1–8.0 are in the range of average plumpness; and those showing a condition of 8.1 or above are obese and usually show internal fat deposits.

The largemouth bass, having more elongated shapes than the shapes of bluegills, have a lower condition index range.

In bass, condition indices of 3.5–4.5 are related to a thin body; bass in the range of 4.6–5.5 are about normal; and those within the range of 5.6 or higher are obese. Bluegills are known to have an annual cycle of condition (Bennett, Thompson, & Parr 1940:6), with condition being lowest during winter, gradually rising in March and April, and reaching a peak in late May or early June at the beginning of the spawning season. During the long spawning season extending throughout the summer, bluegill condition usually drops. Sometimes it rises in late August and early September, dropping again to the winter low. No annual condition cycle has been reported for largemouth bass.

Average indexes of condition are shown in Table 11. Data were taken from creel cards recorded for all fishes by the first junior author when fishermen returned to the laboratory pier with their catches. Length-weight data from fishes caught by anglers during early June, the first

Table 11.—Average index of condition, *C*, of monthly samples of largemouth bass and bluegills taken by fishermen from Ridge Lake during the summer fishing periods, 1963–1969.

Month and Year	Largemouth Bass		Bluegills	
	Num- ber	Average C Value	Num- ber	Average C Value
June 1963	32	4.82	96	6.17
July 1963	17	4.70	128	6.81
August 1963	26	4.08	118	6.37
June 1964	244	4.18	211	7.38
July 1964	134	4.53	245	7.37
August 1964	61	4.46	268	7.30
June 1965	84	4.60	147	7.54
July 1965	74	4.55	246	7.43
August 1965	114	4.44	237	7.44
June 1966	138	4.25	224	8.12
July 1966	93	4.44	270	7.84
August 1966	67	4.20	219	7.65
June 1967	174	4.49	287	8.43
July 1967	104	4.92	246	8.29
August 1967	144	4.77	282	8.11
June 1968	185	4.77	318	8.51
July 1968	92	4.58	337	7.57
August 1968	119	4.53	224	7.57
June 1969	183	4.09	273	7.51
July 1969	82	4.57	224	7.81
August 1969	81	4.71	275	7.96

part of July, and the first part of August were used, and the numbers of fish records ranged between 17 and 337, depending on the numbers available.

Indexes of condition were calculated for bass within the length range of 173–399 mm (6.8–15.7 inches) and for bluegills within the range of 147–246 mm (5.8–9.7 inches). Fishes were separated into 25-mm (1-inch) length groups (e.g., 147–172 mm, 173–198 mm, etc.) so that any great variations in the relative plumpness of these length groups would be exposed. Bluegills were fairly consistent in condition within the size groups recorded, but bass more than 12 inches long were heavier in proportion to their length than were shorter bass. Indices of condition for both bass and bluegills caught by anglers at any one time (within a period of a few days) were quite uniform for their species, although occasionally a few individuals varied widely. The bass condition data in Table 11 emphasizes the fact that in most months the bass averaged slightly *below* normal, or average, plumpness. In general, all bass were thin, but some were more so than others.

During the summer of 1963 the blue-

gills were thin (Fig. 3), but they improved to average plumpness in 1964 before any supplemental feeding was begun. Apparently, the feeding program in 1965 was not reflected in the condition of the bluegills in that year although they were, on the average, somewhat plumper than they were in 1964. The effects of supplemental feeding were evident in the collections for June in 1966, 1967, and 1968 (Fig. 3) when the average C values for bluegills were in the fat category. The condition cycle for this species was evident in most years. Bluegill plumpness in July and August was usually lower, on the average, than it was in June, with mid- and late-summer condition falling below the fat classification in all years except 1967. In 1968, bluegills were in fat condition in June, and large bluegills again reached that level in August. In that same year, a high survival rate occurred among the small bluegills of a very large year class. This high rate of survival became evident in 1969 when many bluegills were too small to interest anglers but were numerous enough to reduce the overall effect of the supplemental feeding.

Fig. 4 shows the average condition for

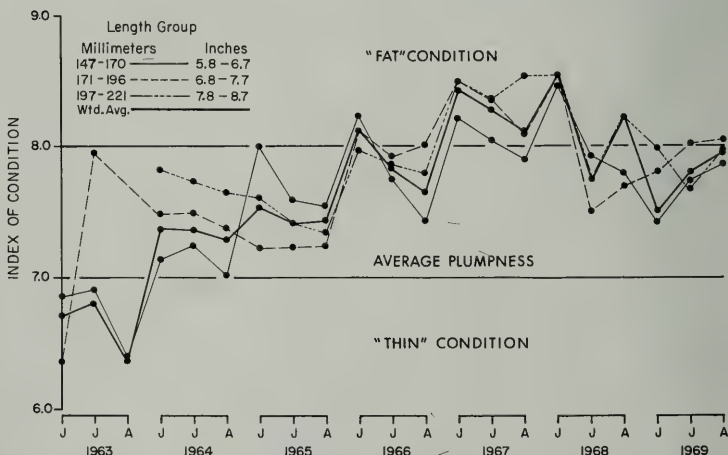


Fig. 3.—Indices of Condition of three length groupings of bluegills and the weighted average for all groupings in summers of the f-d experiment. Supplemental feeding was begun in 1965, and the first drawdown of this program was conducted in the fall of 1965.

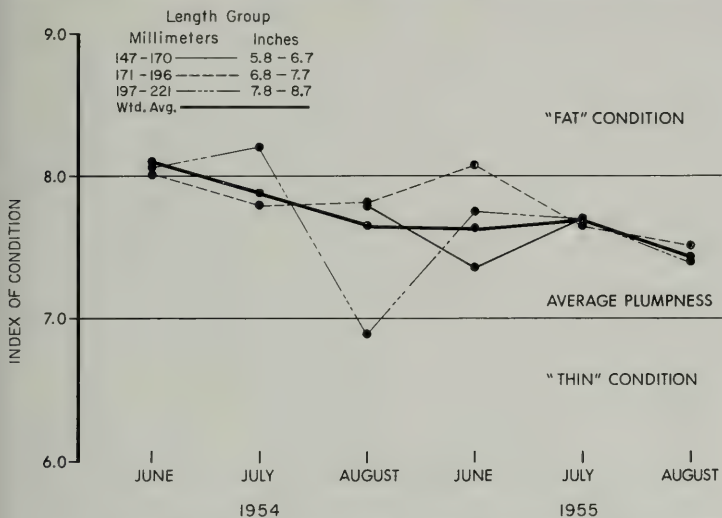


Fig. 4.—Indices of Condition of three length groupings of bluegills and the weighted average for all groupings taken in 1954 and 1955 during a period of annual fall drawdowns but with no supplemental feeding.

three length classes of bluegills taken from Ridge Lake in 1954 and 1955 when this fish population was being subjected to moderate annual fall drawdowns of about 3 meters (Bennett et al. 1969:16) but with no supplemental summer feeding. Bluegills showed an average condition in the fat zone only in June 1954; during the rest of the 2-year span these fish were generally in high average condition. As stated elsewhere, these fish did not appear to be plump.

THE GROWTH OF BASS AND BLUEGILLS IN A FEEDING-DRAWDOWN PROGRAM

Growth rates of largemouth bass and bluegills were estimated from scale analyses and from length, weight, and age data for fishes taken by anglers late in the summers of 1967 and 1968 when fish growth for the season was nearly complete. By averaging the total lengths of bass or bluegills separated into age classes on the basis of the number of annuli on

selected scales, we were able to construct growth curves (Fig. 5, 6, and 7).

The growth of largemouth bass was slow during the f-d period, particularly when compared with that of the period of biennial culling, 1941–1951 (Table 12 and Fig. 5). In the 1941–1951 period the lake was completely drained five times at intervals of 2 years, and each time a census was made of the fish. The method of culling the population after the census has been described (Bennett 1954a:241). The data for the upper growth curve for bass (Fig. 5) were taken from Bennett (1954a:255). This curve shows that bass reached a useful size (254 mm) in less than two growing seasons in the biennial culling period; in contrast, three complete growing seasons were required to obtain 254-mm bass under the f-d program. Also, under this latter program there appeared to be a scarcity of 305- to 380-mm (12- to 15-inch) bass (Table 12). Quite obviously, from the standpoint of growth rate, the f-d program cannot be recommended for bass.

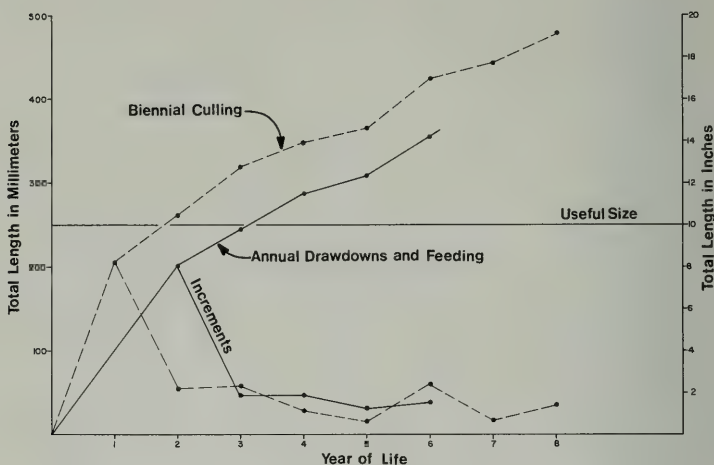


Fig. 5.—Growth rates and annual length increments of largemouth bass under a system of biennial lake draining and culling of small bass and bluegills and under the f-d program.

Table 13 and Fig. 6 and 7 show comparisons of the growth rates of bluegills under the f-d program and under a pro-

gram of drawdowns without feeding and under conditions brought about by stable water levels.

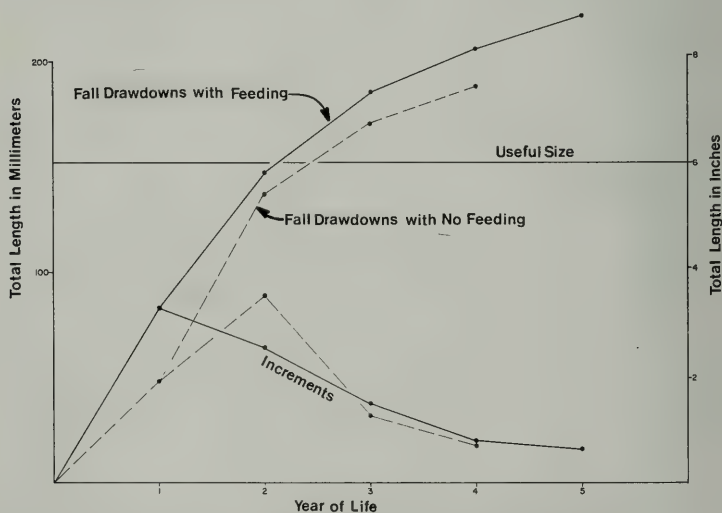


Fig. 6.—Growth rates and annual length increments of bluegills under a system of fall drawdowns without feeding and under a system combining feeding with fall drawdowns.

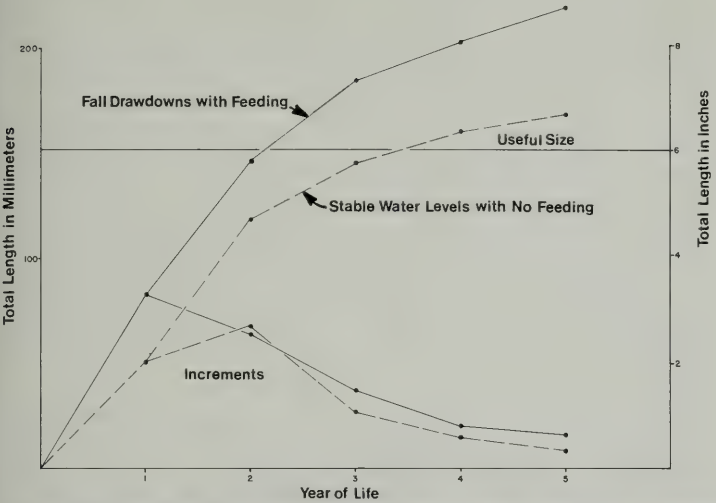


Fig. 7.—Growth rates and annual length increments of bluegills during the f-d program and under stable water levels (1956–1959, inclusive).

Bluegills grew almost as fast when subjected to annual fall drawdowns with no supplemental feeding as they did under the program of supplemental feeding and fall drawdowns (Fig. 6). In both programs useful sizes were attained early in the third summer of life. Under the f-d program, bluegills 4 and 5 years old averaged more than 200 mm (8 inches) in length; however, the average size of the 4-year-old bluegills subjected to drawdowns alone was less than 200 mm, and

there were too few 5-year-olds to give a significant average. Whether supplemental feeding might have been a factor in slowing the mortality rate of the larger, older fish can only be conjecture at this time.

With stable water levels at Ridge Lake in 1956–1959, bluegill numbers increased rapidly, and more than three growing seasons were required for these fish to average 150 mm (Fig. 7). None was able to attain a length greater than about

Table 12.—Average total lengths in millimeters and inches of 405 largemouth bass taken at, or approximately at, the ends of the growing seasons in 1966, 1967, and 1968 during the feeding-drawdown period, and average total lengths of largemouth bass taken under similar circumstances in the 1941–1949 period of biennial draining and culling (from Bennett 1954a:255).

Unit of Measurement	Average Total Length At or Near End of Indicated Growing Season							
	1st	2nd	3rd	4th	5th	6th	7th	8th
Feeding-Drawdown Period, 1965–1969								
Millimeters	...	201	244	287	318	358	...	...
Inches	...	7.9	9.6	11.3	12.5	14.1	...	...
Biennial Culling Period, 1941–1949								
Millimeters	206	262	320	348	363	424	442	478
Inches	8.1	10.3	12.6	13.7	14.3	16.7	17.4	18.8

Table 13.—Average total lengths in millimeters of bluegills captured and aged near the ends of the growing seasons of 1967 and 1968 during the period of supplemental feeding and annual fall drawdowns, of 1958 and 1959 during the period of stable water levels, and of 1955 during the period of annual fall drawdowns without feeding. Annual length increments are also shown.

<i>Period</i>	<i>Number</i>	<i>Year of Life</i>				
		1st	2nd	3rd	4th	5th
Supplemental feeding and fall drawdowns (1967 & 1968 collections)	316	83	147	185	205	221
Length increment		83	64	38	20	16
Stable water levels (1958 & 1959 collections)	326	51	119	146	161	169
Length increment		51	68	27	15	8
Annual fall drawdowns and no feeding (1955 collection)	112	48	137	170	188	...
Length increment		48	89	33	18	...

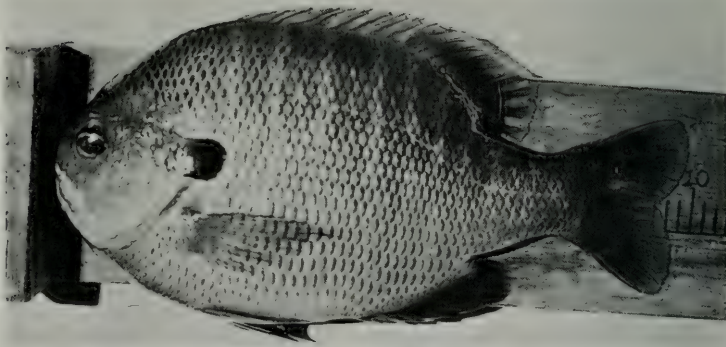


Fig. 8.—A 254-mm (10-inch) bluegill from Ridge Lake weighing 499 grams (1.1 pounds). This bluegill was very fat and had an Index of Condition of 12.

165 mm even though many reached the age of 5 years. Differences in the rates of growth of bluegills in Ridge Lake under differing systems of management apparently are related to the amount of available food and space per individual fish.

If abundant food and space are available, bluegill size must be limited by the length of life of this species and its maximum genetic growth potential. Few bluegills in central Illinois live longer than 5 years and genetically the bluegill is a relatively small fish. Thus, in combining a supplemental feeding program with drawdowns, we are, in theory, projecting a

management technique for producing bluegills of exceptional sizes (Fig. 8).

DISCUSSION

The decision to give warmwater fishes a supplemental source of food in a management program to improve sport fishing depends, first of all, on cost as it is related to benefits. However, data about yield improvement may not be available to the individual fisherman, and he may judge the fishing quality by what he himself catches. Such judging was done by fishermen using Ridge Lake during our experiment.

In waters open to public fishing, usually no attempt is made to harvest more of the available crop of fishes than may be taken by angling; therefore, unless the benefits are readily observable through an improved rate of catch or improved sizes of the fishes caught, or both, fishermen may consider the program a waste of money. As has been mentioned, the cost of the pelleted fish food used in this experiment was about 6 cents per pound, and the feeding rate was 2 pounds of food per acre per day. Thus, the daily cost was 12 cents per acre, or \$1.92 per day for 16-acre Ridge Lake. The feeding program required 1.5 tons of food per year at about \$120-\$130 per ton, representing a seasonal cost of \$11.25-\$12.19 per acre, or \$27.80-\$30.12 per hectare.

Schmittou (1969:312-313) used 2,896 pounds of food costing \$159.28 in 1-acre Pond T₁ over two growing seasons and 8,766 pounds of food costing \$482.13 in Pond T₂ (surface area, 3.5 acres) for five growing seasons. Thus, the food costs per acre per season were \$79.64 for Pond T₁ and \$27.55 for T₂. These costs may be compared with \$11.25-\$12.19 per acre per season for the food used at Ridge Lake.

The results of this f-d program were evident to most, if not all, bluegill fishermen in furnishing them with (i) larger bluegills, (ii) fatter bluegills, and (iii) a larger total poundage of bluegills because of the increased average weight of individuals. Greater numbers of bluegills were taken by anglers in the period of stable water levels, 1956-1959, than were caught in the f-d period, but the fishes taken in the earlier period were hardly more than 152 mm (6 inches) in average total length and their average weight was less than 82 grams (0.18 pound) each. Another benefit cited by fishermen was the improved flavor of the bluegills that fed on the prepared food.

Schmittou (1969:318) fed "balanced" bass-bluegill populations in two "treatment ponds" while following the population changes in a control pond. In his feeding program without drawdowns, there appeared to be a gradual increase

in the number of bluegills and a reduction in the number of bass that eventually would have caused a severe slump in bass fishing. In the Ridge Lake experiment the annual fall drawdowns also upset the bass population dynamics by indirectly causing the production of excessive numbers of small bass, of which only a small percentage attained attractive sizes.

The fact that largemouth bass will not learn to eat pelleted food unless given special training when very small (Snow 1965:193 and 1968:145) reveals the uselessness of simply broadcasting pelleted food in the management of bass for sport fishing.

It is our opinion, after studying the movements of marked bluegills in various parts of the lake, that these fish are fairly sedentary, i.e., their normal range of movements would not insure that individuals from all parts of Ridge Lake would find a feeding area. Therefore, if pelleted food is to be made available to all of the Ridge Lake bluegills, it must be well distributed in shallow water in all parts of the lake.

Once the bluegills have learned to feed on the pelleted food, they will ingest the amount distributed in a relatively short time. There was no particular reason for setting the amount to be fed at 2 pounds per acre per day except that we wished to have the food used as a supplement to the bluegills' natural diet rather than as a substitute for it. However, the weight of bluegills in the 1970 census (78 kg per hectare, or 69 pounds per acre) was about one-third of the maximum standing crop found in any past census (223 kg per hectare, or 200 pounds per acre). Thus, the daily quota of pelleted food represents about 2.5 percent of the total weight of bluegills. The effect of the drawdown in thinning the bluegill population was to increase the amount of food available to each fish from about 1.0 to 3.0 percent of body weight per day.

Various companies in the business of preparing and marketing animal foods usually have one or more types of pelleted fish foods. Generally these preparations consist of one or two grades of "trout" food and at least one, and sometimes two,

grades of "catfish" food. The trout foods are usually more expensive than those for catfish and are more "complete" fish diets because trout have been fed on prepared diets for more years than have catfish and more research has been done on their specific food requirements.

During the development of techniques for the culture of channel catfish in cages, many fish were confined in relatively small spaces with little chance of obtaining a significant amount of natural food from the ponds in which the cages were floated. In this situation foods that were quite adequate for free-swimming channel catfish lacked certain food elements that the free catfish were able to forage from pond sources. Very little is known about the nutrition requirements of bluegills, but it seems reasonable to assume that the food requirements of caged and uncaged bluegills might be similar to those of catfish, i.e., caged bluegills would also require a more nearly complete diet than would free-swimming bluegills.

The drawdown, when combined with a feeding program, is a money-saving operation because it limits the survival of successive year classes of bluegills to the numbers that can be utilized in the fishing program. Thus, the bluegills that survived the drawdowns always had an adequate supply of food for rapid growth and were abundant enough to satisfy the needs of anglers.

Diminishing the aquatic habitat selects against the survival of smaller fishes in two ways. First, it forces the small fishes away from the shore shallows into open water with little or no protective cover in an environment that may be entirely strange to them. Here they become prey to larger fishes and other aquatic vertebrates and invertebrates such as crayfish. Second, it strands the smaller fishes in mats of settling rooted aquatic plants or in pockets of water in an uneven lake bottom which dry up in a few hours or days. The relative importance of these two phenomena in reducing the numbers of smaller fishes is conjectural, however, as much depends on the normal behavior patterns of the species involved. Those that tend to avoid very shallow water are

decimated more by direct predation than by becoming stranded, and vice versa.

To some pond owners a fall drawdown may present a problem because many ponds are not equipped with controlled outlets; therefore, drawdowns are impossible except through pumping or siphoning. Often when a pond is being built, the owner is operating on a limited budget, and the elimination of the drain outlet appears to be one way to cut expenses. This view is unfortunate because the use of the drawdown as a fish management technique has become well established (Bennett 1971:209-219). In fact, it is considered the single most important operational procedure for eliminating overpopulation and stunting among the fishes in artificial ponds and reservoirs.

The procedure is simply to open the outlet valve in the dam and lower the water level until the surface area of the lake or pond is between one-fourth and three-fourths that of the full lake, depending on how severe an effect is desirable. It is usually unnecessary to build a weir in the outlet to prevent the larger fishes from leaving the lake because they will not go out of the outlet until the water level becomes much lower than the level which results in a 75-percent reduction in the lake surface area. Presumably, the larger fishes will not leave because they do not immediately recognize the danger of becoming stranded in the lake basin. If the outlet valve in the dam is at the lowest level of the lake basin and the lake is of the eutrophic type, a drawdown in summer or early fall will release oxygen-deficient water which also may contain methane, hydrogen sulfide, carbon dioxide, and other anaerobic decomposition products. This water may be toxic to fishes immediately below the outlet and is certainly uninhabitable for fishes attempting to enter or leave the lake through the outlet.

It is always advisable that those responsible for the operation of a drawdown inspect the surviving population of fishes to make certain that the expected results are occurring. In some instances it may be necessary to supplement a draw-

down with seining, as Hulsey (1957:286) arranged for in Nimrod Lake, to remove a large population of carp or buffalo or suckers that cannot be stranded and are too large to become prey to fishes or other aquatic animals. Even excessively large populations of stunted sunfishes may require supplemental cropping, particularly when they are living with relatively small numbers of large bass, of which there are too few to make impressive inroads on the hordes of sunfishes. In both cases boat-mounted electric shockers may be used effectively in thinning the stunted or undesirable fishes, because during a drawdown the fishes are concentrated in such small areas that large numbers may be stunned within a relatively short time. Where seine hauls have been planned for reservoir basins before the water has been impounded, small-meshed drag seines may be used to help reduce the numbers of undesirable fishes.

In managing a lake or pond for sport fishing, it is desirable to manage all important species that are present. This we were unable to do with our f-d program. The program was effective in producing superior bluegills, and probably superior catfish, but it was not so for largemouth bass. Perhaps a severe fall drawdown each year is unnecessary, and one in 2 or 3 years with annual summer feeding might improve the size of the bass caught without greatly reducing the average size of the bluegills. In another direction, the maintenance of a population of channel catfish of at least 100 per hectare might add a new interest for fishermen.

SUMMARY

1.—After a draining census in 1963, Ridge Lake was restocked with 2,386 largemouth bass, 4,492 bluegills, 1,335 warmouths, 11 channel catfish, and 1,020 lake chubsuckers, making a total of 9,244 fishes weighing 510.6 kg (1,125.5 pounds). This was 78.8 kg per hectare, or 70.3 pounds per acre. In the census preceding this restocking this lake was found to contain 287 kg per hectare, or 256 pounds per acre, almost four times

the weight of fish returned to the lake. In 1969, 2,000 additional channel catfish were stocked.

2.—The population of fishes was allowed to expand for two growing seasons (1963 and 1964) without drawdowns or supplemental feeding but with the usual controlled public fishing during the summer months. The hook-and-line catch in 1963 and 1964 was below the average for the preceding 20 years.

3.—Beginning in late May 1965, and continuing each year during the 3 summer months, 1965 through 1969, the fish were fed daily on a commercial pelleted fish food (32 percent protein) at the rate of 2 pounds per acre per day. Food was spread in the shallows in all parts of the lake. The food cost was within the range of \$27.80–\$30.12 per hectare per season (\$11.25–\$12.19 per acre per season).

4.—Each year, beginning in September 1965, the lake level was lowered:

4.6 meters (15 feet) in 1965, leaving a surface area of 2.12 ha

3.0 meters (10 feet) in 1966, leaving a surface area of 4.5 ha

3.0 meters (10 feet) in 1967, leaving a surface area of 4.5 ha

4.6 meters (15 feet) in 1968, leaving a surface area of 2.12 ha

4.3 meters (14 feet) in 1969, leaving a surface area of 2.76 ha

The level was maintained until the water temperature in the lake was about 13° C. (57° F.) in October, when the lake was allowed to refill.

5.—In March 1970, the lake was drained to make a census of the fishes. The lake contained 2,420 bass, 9,546 bluegills, 556 warmouths, 1,477 channel catfish, 232 lake chubsuckers, and 3 fishes of other species, a total of 14,234 fishes weighing 1,440.0 kg (3,175.3 pounds).

6.—The catch of largemouth bass during the seasons 1965–1969, inclusive, was composed mostly of small fish. The f-d program resulted in the production of excessive numbers of small bass but generally did nothing to improve bass fishing.

7.—The fishermen's catch included more than twice as many large bluegills (152 mm or longer) as it did smaller ones during the 1965–1969 period. Blue-

gills of desirable sizes averaged 127 grams (0.28 pound) each.

8.—Neither warmouths nor channel catfish produced large hook-and-line yields because their numbers were always small. Channel catfish produced a small year class in 1963 or 1964, and this year class appeared in the catch in 1966–1969, inclusive. The catfish stocked in 1969 were too small to appear in the 1969 catch.

9.—During years when the water level in Ridge Lake remained fairly constant, bluegill numbers increased to 50,000 in one 2-year period and to 66,000 in another, to 86,000 in one 3-year period, and to 93,000 in a 4-year period. Annual fall drawdowns of 4.6 meters reduced the bluegill population to 7,500, those of 3.0 meters to 17,000 bluegills, and the 4.3-meter drawdown reduced the population to 9,500 bluegills. These drawdowns apparently had little effect on largemouth bass numbers.

10.—The average hook-and-line yield of bass in the 5 f-d years was only 18.0 kg per hectare (16.1 pounds per acre). This yield was below the average for 3 drawdown years (1952, 1954, and 1955) and 3 stable water level years (1957, 1958, and 1959). The average bluegill yield under the f-d program was 71.6 kg per hectare (63.9 pounds per acre), higher than the catch in any other period.

11.—The average index of condition of largemouth bass in the f-d period was

slightly *below normal*. Average bluegill condition was “fat” in June of all f-d years except 1965 and 1969. Usually the average bluegill index of condition was lower in July and August, which followed a previously observed condition cycle for that species. The condition of bluegills in 1954–1955 with fall drawdowns, but without supplemental feeding, was “fat” in June of 1954 but only reached “high average” plumpness for July and August of 1954 and for all of the summer of 1955.

12.—Largemouth bass growth was slower during the f-d period than during the period of biennial lake draining and culling of the fish population. Bluegills grew somewhat faster during the f-d period than they did during the program of drawdowns without feeding. They appeared to live longer during the f-d period and therefore attained larger sizes. They grew much faster under the f-d program than they did when water levels were stable.

13.—The pelleted food for the f-d program cost about 12 cents per acre per day, or about \$11.25–\$12.19 per acre per season. Fishermen were enthusiastic about the program because they were able to catch larger and fatter bluegills, and they believed that the pelleted food improved the flavor of these fish. Feeding bluegills without fall drawdowns would probably be wasteful because the bluegill population would expand faster than the food supply.

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This report is printed by authority of the State of Illinois, IRS Ch. 127, Par. 58.12. It is a contribution from the Section of Wildlife Research of the Illinois Natural History Survey.

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The Reproductive Cycle of the Raccoon in Illinois

Glen C. Sanderson
A. V. Nalbandov

ALTHOUGH THE RACCOON (*Procyon lotor*) is a commonly recognized, widely distributed, and abundant North American mammal, little has been known about its reproductive cycle except the season of birth, the number of young per litter, and the duration of the gestation period. Basic information on the length of the estrous cycle, whether ovulation is spontaneous or induced, the period of sexual activity in the male, the occurrence of pseudopregnancy, the roles of the various hormones in reproduction, and the anatomy of the reproductive tracts has been either lacking or fragmentary.

The objectives of this study were to gather data on the reproductive cycle and the basic anatomy of the reproductive system of the raccoon and to investigate those aspects of the raccoon's reproductive physiology that gave promise of increasing our knowledge in the general field of mammalian reproductive physiology. This study was part of an effort to obtain a refined understanding of the population dynamics of the species. Other aspects of the study will be published elsewhere.

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Frontispiece.—Cages used to hold raccoons in Urbana, Ill. Each double cage held either one pair, one female and her young, or 1-3 adult raccoons in each half. The outside dimensions of the cages were 3 feet (width) X 4 feet (height) X 6 feet (length). Each cage was divided crosswise through the middle with wire and had a nest box on each end. The wire was 1.5-inch mesh, 14-gauge hexagonal netting. The nest boxes had wire bottoms, and wooden bottoms were inserted on top of the wire in winter. A hinged wire top on each nest box fitted under the removable lid.

R. R. Graber, and others. Helen C. Schultz of the Survey staff and Robert M. Zewadski, Associate Technical Editor of the Survey, edited the manuscript.

Dr. H. W. Norton and Dr. A. Sydney Johnson, Associate Director, Institute of Natural Resources at the University of Georgia, Athens, reviewed the manuscript and made many valuable suggestions.

We are especially grateful to Clifford, Albert, and Robert Perardi (Perardi Brothers Fur and Wool Company, Farmington, Ill.) for their active and enthusiastic cooperation with our study.

METHODS

SEASONAL CYCLE OF THE GONADS

Each year from 1955 through 1961 the senior author examined dead raccoons at a number of fur houses in central Illinois. The majority of the raccoons were examined at Farmington in Fulton County and Colchester in McDonough County. Most or all of these animals came from within the range of *Procyon lotor hirtus* (Goldman 1950:24). During the hunting and trapping season, which usually occurred during November through January (but occasionally included late October), large numbers of recently killed raccoons were sold to fur-buying establishments and pelted. Often a majority of the acceptable carcasses were dressed and frozen prior to being sold for human food. Thus, from the large number of raccoons examined, numerous data were recorded and many organs suitable for gross examination were collected as the animals were being skinned.

The present report deals principally with the reproductive organs of the raccoon. Before the animals were skinned, one testis and epididymis were removed from each male, and the condition of the nipples of each female was recorded. All pertinent information was recorded separately for each animal. After the raccoons were pelted, the complete reproductive tracts were removed from fe-

males and were placed separately in 1-pint plastic bags to prevent the tissues from drying. Each plastic bag was placed in a small paper bag on which the data were recorded.

The specimens were usually examined in the laboratory the day after collection but sometimes were examined on the day they were collected. The testes were weighed to the nearest 0.1 gram. A drop of fluid collected from the tail of the epididymis was diluted with a drop of normal saline solution and examined under the microscope for the presence of sperm. Both ovaries were examined visually and weighed to the nearest 0.1 mg.

Raccoons found dead or collected by trapping and shooting specifically for autopsies were processed in the same general manner as those examined in fur houses. A small number of raccoons, obtained from sources other than fur buyers, came from the southern and eastern sections of Illinois within the range of *P. l. lotor* (Goldman 1950:24).

Gonads from both sexes were collected from adult and juvenile raccoons each month. Several gonads were removed immediately after the deaths of the animals and were preserved and prepared for histological study. The average monthly weights of the gonads from all of the raccoons studied, both those freshly killed and those dead for several hours, were used in constructing graphs showing the seasonal gonadal weights for juveniles and adults of both sexes. Histological examinations of the testes, epididymides, ovaries, and uteri contributed information regarding the seasonal sexual cycle.

CAPTIVE RACCOONS

For many phases of the study captive raccoons were kept in outdoor cages in Urbana, Ill. Most of these animals were trapped in the wild, both as adults and juveniles, and some as small young, mostly in Champaign, Piatt, Edgar, and Carroll counties, Ill. We estimated the ages of wild raccoons at the times of their cap-

ture (Sanderson 1961a). Some animals used for the study were born in captivity—some were conceived in captivity and others were born in captivity to females that were pregnant when captured.

Captive raccoons were usually paired and held as one male and one female per cage. Pregnant females were isolated prior to parturition; the males were not returned while the young were with the females. Some females were isolated to determine whether ovulation in the raccoon is induced or spontaneous. In some cases three or more animals—juveniles of both sexes and surplus males—were held in a single cage.

The captives were given fresh food and water daily. The main diet was Dog Checkers or Laboratory Checkers, manufactured by the Ralston Purina Company. Occasionally the diet was supplemented by chickens, fish, eggs, and other available fresh foods.

Captive raccoons that died or were killed were processed as described above, except that all of the gonads, after being weighed, were preserved for histological study. Usually a section of the uterus and occasionally accessory organs of the reproductive tract were also preserved for histological examination.

Males

The annual reproductive cycle in several captive male raccoons was determined by restraining each male in a wire cone at irregular intervals throughout the year and collecting a drop of fluid from the tail of the epididymis. The tail of the epididymis was forced against the skin of the scrotum; then a pointed scalpel was used to prick through the skin, and a drop of fluid was collected on a glass slide. The drop was diluted with normal saline solution and examined under the microscope for the presence of sperm. After the collection of the epididymal fluid, the animal was returned to its cage with no further treatment. No infection or other troubles resulted from this treatment.

Occasionally, a captive male, or a wild

male that had been livetrapped and was to be released at the point of capture for another phase of the study, was unilaterally castrated to obtain a testis and epididymis for study. Captive males that fathered young were assumed to have had sperm in their epididymides at the time that they impregnated the females.

Females

The reproductive cycle of captive female raccoons was studied by examining the ovaries and uteri during laparotomies of anesthetized animals. The anesthetic used was pentobarbital sodium administered at the rate of 1 cc per 4 pounds of body weight. Given intraperitoneally, it usually produced surgical anesthesia in 10–30 minutes; however, individual responses to the anesthetic varied, and animals that required more anesthetic were given larger doses the second time laparotomies were performed.

The raccoon is resistant to infection and withstands surgical incursions well. Instruments were washed in 70-percent alcohol but were not sterilized. As many as 12 laparotomies were performed on one female over a period of several months, sometimes on subsequent days, sometimes two or three times in 1 week, but usually from 2 weeks to several months apart. Animals were usually given penicillin after each operation although no infections developed when it was not used. Surgical silk or cat gut was used to close the peritoneal linings and muscle; these sutures were not removed until a subsequent laparotomy was performed. Wound clips, used to close the skin, were removed approximately 10 days after the operation.

To examine ovaries for evidence of ovulation, it was usually necessary to slit the ovarian capsules. Because the cut edges of the capsules did not always grow together, this procedure was omitted when examining females that were being held to produce young. The uterus was gently withdrawn from the body cavity for examination and gross measurement.

In several cases one or both ovaries were removed for study. Uterine sections were taken from living females for histological study of the development of the endometrium.

MEAN BIRTH DATE OF RACCOON LITTERS

The mean date of birth was determined for 20 litters conceived in the wild in the northern half of Illinois. Of these 20 litters, 7 were born in captivity. The potential birth dates of the others, most of which were examined in female raccoons found dead along roadways, were estimated by measuring the uterine swellings in the manner described by Llewellyn (1953:321). Data obtained during the present investigation were also used in estimating the probable birth dates. Because Llewellyn (1953:321) recorded measurements of only three embryos in one litter at three different stages and at birth, several embryos were measured in captive females during this study. Although the dates of conception were not known, the maximum measurements of the uterine swellings were plotted in relation to the number of days prior to the known birth dates. Many wild females were examined throughout the year for pregnancy, lactation, and the presence of fresh placental scars and corpora lutea. This information helped to determine the limits of the breeding season in wild raccoons.

SECONDARY SEX RATIOS

Secondary sex ratios were obtained by examining 83 embryos and young at birth in 26 litters and by determining the sex of 54 wild raccoons less than 2 months old from 23 litters. Chi-square tests were used to test whether the sex ratio of the wild young less than 2 months of age was different from equality and from the ratio of the embryos and young at birth.

ESTROUS CYCLE AND OVULATION

Estrous Cycle

Estrous cycles were determined for individual captive female raccoons by

examining the ovaries at or near ovulation and then reexamining the ovaries at intervals until the animals ovulated again.

The raccoon's main breeding season was interrupted throughout much of Illinois by colder-than-normal temperatures and deep snows in 1960. Observations of live-trapped raccoons and the body weights of young, wild raccoons weighed during the fall and winter of 1960 indicated that some raccoons were born later than normal during that year. Lenses collected from several young raccoons during the hunting and trapping season of 1960-1961 were used to estimate the months of birth for these juveniles (Sanderson 1961b:482-485). The time intervals between the peaks of estimated birth dates were assumed to represent the average interval between ovulations for wild raccoons in central Illinois.

Cotton swabs were used to take daily vaginal smears from several captives in an attempt to delineate the estrous cycle. Observations of vulval swelling, size and pigmentation of the nipples, and general disposition of the animals were made each time the animals were handled. Vaginal tissues were removed from several females for histological study.

Ovulation

Each of two females was placed alone in a small cage in the fall of 1960 to obtain information on the mechanism of ovulation and on pseudopregnancy. These females could see other raccoons but could not come into physical contact with them. Also, one pet female, reported by the owner to have had no contact with other raccoons, was observed. Individual corpora lutea were studied in these females during a series of laparotomies.

Some of the corpora lutea in the ovaries of three females were marked with India ink—and the locations of all corpora lutea were mapped. By following the fate of the marked and mapped corpora until they disappeared, we found that mapping the corpora lutea was as

reliable a method of determining their life-spans as was marking them with ink. Mapping was used in subsequent studies. At each initial observation the ovary was forced through the slit ovarian capsule, the corpora were examined for color and measured grossly, and their locations in the ovary were mapped.

INTERSTITIAL TISSUE

Ovarian interstitial tissue was studied in wild raccoons on which observations as to pregnancy and lactation had been made, in several captive females treated with various hormones prior to the removal of the ovaries, and in untreated captives whose breeding histories were known. A uterine section was usually obtained when ovaries were collected, and the condition of the endometrium was studied in relation to the degree of development of the interstitial tissue. Representative sections selected from each ovary and uterus were photographed by mounting the slide in the carrier of a photographic enlarger and projecting the image directly onto 4- X 5-inch contrast process ortho sheet film. Prints 8 X 10 inches were made on F5 Kodabromide paper. By examining the photographs, we determined the abundance and distribution of cells of each type in the interstitial tissue in relation to the development of the endometrial glands, the time of year, the age of the animal, and the stage of the reproductive cycle.

HISTOLOGY

Tissues were preserved in Bouin's solution or in 10-percent formalin neutralized with either $MgCO_3$ or $CaCO_3$. The organs preserved in Bouin's solution were left for an indefinite period, but those preserved in 10-percent formalin were transferred to 70-percent alcohol after 48-72 hours. With a few exceptions, all tissues prepared for histological examination were stained with hematoxylin and eosin. The ovaries of a few females that had died some time prior to the preservation of the organs

were sectioned at 15-20 microns; the number of corpora lutea was our main interest in these ovaries. In all other cases the sections were cut 6 microns thick. The preserved organs were embedded in paraffin and sectioned and mounted by routine methods.

PLACENTAL SCARS

In dead female raccoons placental scars were counted, using transillumination. The uterus was then slit and the inside surfaces were examined for scars.

In captive pregnant females the uterine swellings were measured and the locations of the embryos were mapped during laparotomies. After parturition the presence and persistence of placental scars at the sites of known placental attachment were studied during a series of laparotomies. The scars were examined in living animals by gently pulling the uterus far enough out of the body cavity to allow it to be transilluminated. Uterine sections containing scars at various stages were removed from living females at intervals for histological study.

MORPHOLOGY OF THE REPRODUCTIVE TRACTS

Males

A few complete male reproductive tracts were removed and preserved for histological study. The entire tract from one male, and individual accessory organs from a few additional males, were sectioned. India ink was injected into one vas deferens of a fresh specimen until the ink ran out the urethral opening of the penis. The tract was then preserved and sectioned for histological study to trace the duct system, containing particles of India ink, through the prostate gland.

A schematic diagram of the male reproductive system was sketched from a fresh specimen that had been partially dissected but was sufficiently undisturbed to show its relationships to adjacent structures. A complete reproductive tract that had been dissected and preserved was used for reference.

Females

A schematic diagram of the reproductive tract (from one female) was prepared from a fresh tract that had been sufficiently dissected to reveal its conformation but that maintained its position relative to adjacent structures. One entire tract that had been removed and preserved was used for reference.

EFFECTS OF CASTRATION

Males

Four captive male raccoons were castrated at ages ranging from 72 days to approximately 9 months to study the effects of castration on the development of the penis bone, the opening of the preputial orifice, and the age at which the epiphyses close in the radius and ulna. These studies were not completed because the four animals died of various causes at different ages; the one that lived the longest attained an age of approximately 22 months.

Females

One female raccoon, born in captivity, was 3 months of age when castrated; the second, born in the wild, was estimated to be 4 months old when castrated. Several adult females were also castrated to study the effects of castration on vaginal smears, the vaginal epithelium, the uterus, and the closure of the epiphyses in the radius and ulna.

Vaginal tissues and uterine sections were taken from castrated females at intervals. These tissues were prepared for histological study and used for comparison with similar tissues from females believed to be anestrus. The females castrated as adults were also used to study the effects of various exogenous hormones on vaginal smears, the vaginal epithelium, and the development of the endometrium.

Two pregnant females were castrated as the first phase of a study of the effect of castration on pregnancy. The first female, with four embryos, was castrated 38 days (estimated time) after conception. The second female, with five em-

bryos, was castrated approximately 11 days after conception. These females were observed daily after castration for signs of abortion. A second laparotomy was performed on the first female 21 days after castration and on the second female 19 days after removal of the ovaries.

EFFECTS OF EXOGENOUS HORMONES

Males

Two captive adult male raccoons were used for preliminary studies of the effects of androgen on spermatogenesis. Beginning in August, near the midpoint of sexual inactivity, injections of testosterone cyclopentylpropionate (Res. No. 8961-1, Upjohn) were administered to both of these males. The first male received seven subcutaneous injections of 30 mg each at 3-day intervals.

Immediately before the first injection of the hormone the left testis and epididymis were removed from each animal. The testis was weighed and a smear from the tail of the epididymis was examined for the presence of sperm. Each testis and epididymis was prepared for histological study.

The first male was killed 21 days after receiving the first androgen injection, and the right testis, right epididymis, and the prostate were removed. The testis was weighed and a smear from the tail of the epididymis was examined for sperm. The second male was similarly treated but received four injections of 12 mg each and was killed 15 days after the first injection was administered.

Females

Several attempts were made to cause the growth and development of Graafian follicles and to cause ovulation by injecting various hormones into female raccoons. The hormones used were pregnant mare's serum (PMS, Upjohn), the pituitary gonadotropins (FSH and LH, Armour), estradiol cyclopentylpropionate (ECP, Upjohn), estradiol valerate (estradiol, Squibb), hydroxyprogesterone caproate (progesterone, Squibb), chorionic gonadotropin (CGH, Up-

john), and human menopausal gonadotropin (HMG-J5, Statens Seruminstitut, Copenhagen). Because these hormones were administered by many different routes and at many different dosage levels and time intervals, the methods used are discussed in connection with the particular animals involved or are given in the tables where the results from the individual animals are summarized.

UTERINE MILK

Studies were made to determine the hormone or hormones responsible for the secretion of uterine milk by the endometrial glands and to learn the nature of this secretory material. Ovaries and uteri were sectioned and stained from 18 raccoons—all were collected during the breeding season and some of them were pregnant—in which corpora lutea were present and from 89 raccoons—collected throughout the year—whose ovaries contained no corpora lutea. None of these 107 raccoons had been injected with hormones. In all cases the endometrial glands were examined for the presence of secretory materials.

Various hormones were administered to castrate females, uterine sections were removed at varying time intervals, and the endometrial glands were examined by histological methods for the presence of secretory material. The hormones used on individual castrate and intact females to study hormonal control of the secretion of uterine milk were progesterone and ECP, ECP alone, and progesterone alone; however, progesterone alone was not given to any castrate animal for a sufficient time to determine whether it would cause the uterine glands to secrete. Also studied were the direct and secondary effects of PMS, FSH, and LH, used primarily in attempts to cause the growth of Graafian follicles and to cause ovulation, and the production of secretory material by endometrial glands in intact females.

Methods described by Pearse (1960: 265-271) and Lillie (1954: 274-299)

were used to demonstrate the nature of the material observed in the lumina of the endometrial glands. Uterine sections from three female raccoons that had material present in the endometrial glands were used. The uterine section from one was fixed in 10-percent formalin neutralized with CaCO_3 . The uterine section from another was fixed in Bouin's solution, and the section from a third was fixed in 10-percent formalin neutralized with MgCO_3 . All of these tissues were imbedded in paraffin for sectioning, and control slides were used in each case.

RESULTS AND DISCUSSION

SEASONAL CYCLE OF THE GONADS

Males

The age at which male raccoons reach sexual maturity may vary from one region to another. In Michigan, on the basis of meager circumstantial evidence, Stuewer (1943b: 72) concluded that males "are probably not sexually mature by the first breeding season after their birth." In Illinois Pope (1944: 91) had two captive males—of parent stock supposedly "from northern Illinois or some adjacent region"—that mated successfully before they were 1 year of age.

Stuewer (1943b: 63) reported that the testes of juveniles and yearlings were in an abdominal position; those of adults were usually descended during the breeding season and, though variable in position, during the remainder of the year were most often in the coelom. Stuewer's evidence suggested that testis size might reflect the capacity to breed. He measured the lengths of testes in the scrotum with an accuracy of approximately 5 mm. Stuewer (1943b: 64) concluded that if "testis size is significant, males are probably capable of breeding at all times of year after reaching maturity." Asdell (1946: 136), on the basis of Stuewer's work but omitting his qualifications, stated that the male raccoon was capable of mating at any time. Nalbandov (1958: 162) cited the male raccoon as

a species in which spermatogenesis is continuous although the breeding season of females is restricted to late winter and early spring.

The data in Table 1 and Fig. 1 show that raccoon testes grew at a rather uniform rate from birth until about 10 months of age (through the February after birth), when the average weight of one testis was 5.6 grams. The testes of juvenile males showed the most rapid gains in weight between December and February. The average weight of a testis from a juvenile male in November was only 30 percent of the average weight in February. The sample sizes for February, March, and April were small, but there was an indication that the weights of testes in juveniles declined after February. After April testicular weights of juveniles were included with those of adults because a majority of the juvenile males were sexually active by April.

In our experience raccoon testes were nearly always found in the scrotum, even at birth, Stuewer's (1943b: 63) statements to the contrary notwithstanding. They were more prominent in adults than in juveniles, and most prominent in adults during the breeding season. Even in immature animals the testes were rarely withdrawn into the body cavity.

In Illinois a majority of the male raccoons reached sexual maturity as yearlings. Although the presence of sperm in the epididymis does not necessarily indicate sexual potency, it does indicate that an animal is in or approaching the period of sexual activity. No juvenile male had sperm in its epididymis prior to October (Table 1). In October the epididymides of about 9 percent of the juveniles contained sperm; by February this figure had increased to 87 percent. An extrusible penis was another indication of a juvenile's stage of sexual development (Sanderson 1961a: 14). Occasionally, a male was found with a non-extrusible penis but with sperm in its epididymides. Among juvenile males, 5 percent had extrusible penes in September. This figure had increased to about 67 percent by February and March but declined slightly in April. These data indicated that, in Illinois, from one-half to two-thirds of the juvenile male raccoons are sexually mature by the time they are 1 year old (Table 1). By sexually mature we mean that the male has an extrusible penis and a relatively high concentration of sperm in the epididymides.

Comparison of data from juvenile and adult male raccoons shows that juveniles became sexually mature 3-4 months later in the year than did adults. Several

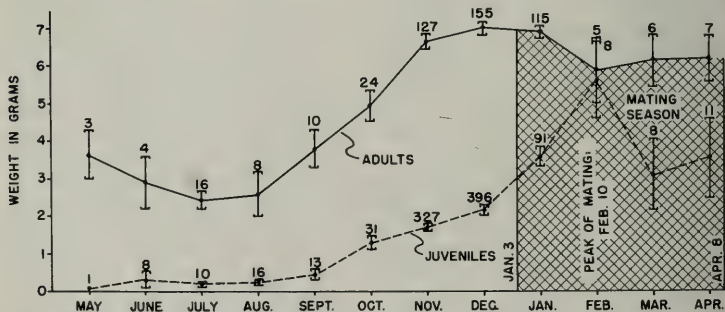


Fig. 1.—Seasonal variations in the average weight of one testis in adult and juvenile raccoons. With each mean are the number of observations and a vertical line representing the mean plus or minus one standard error. All animals were taken in Illinois from November 1955 through April 1961. The data are given in Table 1.

Table 1.—Average monthly testis weights of raccoons and the occurrence of sperm in the epididymis.^a

Time	Juveniles ^b				Adults ^b			
	Average Weight of One Testis in Grams	Standard Error	Range	Percent with Sperm in Epididymis ^c	Percent with Penis Extrusible ^d	Average Weight of One Testis in Grams	Standard Error	Range
At birth	0.0042(1) ^e			0 (1)	0 (1)			
May ^f	0.01 (1)			0 (1)	0 (17)	3.63 (3)	0.64	2.8–4.9
June	0.34 (8)	0.24	0.1–2.0	0 (1)	0 (13)	2.92 (4)	0.68	2.0–4.9
July	0.21 (10)	0.03	0.1–0.4	0 (10)	0 (51)	2.45 (16)	0.22	1.3–4.4
August	0.24 (16)	0.04	0.1–0.4	0 (16)	0 (32)	2.60 (8)	0.58	0.8–6.0
September	0.46 (13)	0.12	0.2–0.4	0 (13)	5 (39)	3.81 (10)	0.47	1.1–5.9
October	1.26 (31)	0.18	0.3–3.7	9 (32)	11 (47)	4.96 (24)	0.36	1.7–7.6
November	1.68(327)	0.09	0.1–7.3	8(323)	14(314)	6.65(127)	0.16	2.6–11.3
December	2.15(396)	0.10	0.1–7.1	24(395)	25(396)	6.99(155)	0.15	1.2–13.6
January	3.57 (91)	0.25	0.2–9.8	32(118)	29(120)	6.86(115)	0.16	2.7–11.0
February	5.61 (8)	0.99	0.4–9.2	88 (8)	67 (12)	5.84 (5)	0.83	3.3–7.6
March	3.05 (8)	0.86	0.9–5.0	57 (7)	67 (9)	6.13 (6)	0.69	4.6–8.7
April	3.55 (11)	1.03	0.6–8.7	33 (10)	50 (8)	6.14 (7)	0.58	4.5–8.9

^a All raccoons were from Illinois and were collected from November 1955 through April 1961.^b A juvenile was 0–12 months of age; an adult was more than 1 year old.^c Determined by microscopic examination of a drop of fluid from the tail of the epididymis.^d Most adults have easily extrusible penes; rarely is a 13- to 16-month-old male found with a nonextrusible penis.^e The numbers of observations are in parentheses.^f Most juveniles are 1 month old in May.

juvenile males had no sperm in their epididymides during the peak of the breeding season but became sexually mature after most of the breeding had been accomplished. At least some adult males were incapable of breeding when the second and third ovulations occurred. Hence, we believe that a majority of the second litters born to raccoons are sired by yearling males.

This study is the first to establish that seasonal variations occur in the testis weights of raccoons (Fig. 1). The average weights of the testes of adult males were minimal in June, July, and August, began increasing during September, and reached their peak in December. Among adults the maximum average weight of one testis was nearly three times the average minimum weight. A decline in testis weight appeared to occur prior to the peak of the breeding season in Feb-

ruary; however, our sample sizes for February, March, and April were small. Testes continued to decline from their peak weight in December to a low point in July. In adults there was a positive correlation between testis weight and the presence of sperm in the epididymis (Fig. 2).

Four males were unilaterally castrated on different dates. The second testis was removed from each at a later date. The weights of these testes are shown in Table 2. In many species the removal of one gonad causes the second one to hypertrophy, but our observations on the effects of unilateral castration in the raccoon on the weight of the remaining testis are inconclusive. The remaining testes in the two adult males castrated unilaterally in July showed greater-than-average increases in weight from July to December. A greater-than-average

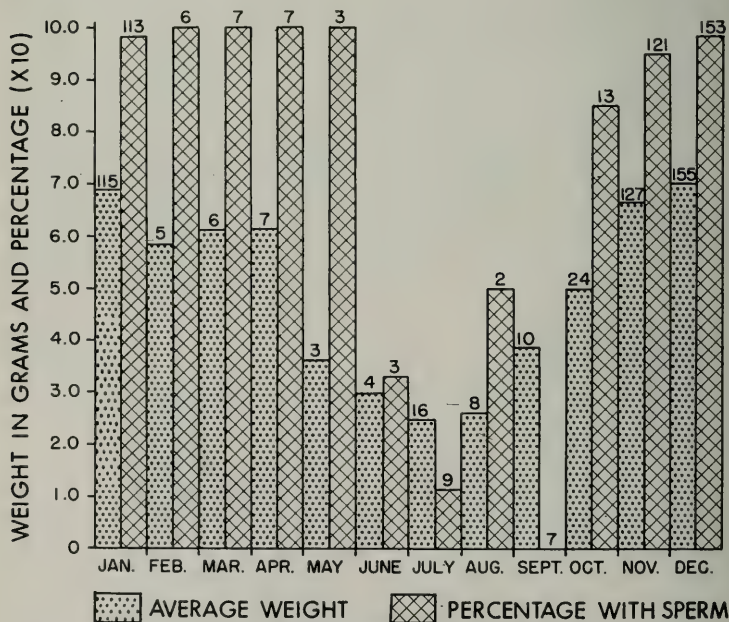


Fig. 2.—Seasonal variations in the average weight of one testis taken from adult raccoons and the percentage of adults with sperm in the epididymis. The numeral at the top of each bar indicates the number of observations.

Table 2.—Testis weights of four raccoons, showing seasonal changes in individual animals.

Raccoon Number and Type	Estimated Age in Months	Date	Weight of One Testis in Grams	Sperm Present or Absent ^a
1771 (wild)	15	7-18-57	1.5	—
	20	12-23-57	9.6	+
1783 (captive)	15	7-19-57	2.6	—
	20	12- 6-57	9.6	+
1803 (captive)	7	11- 6-57	1.5	—
	9	1- 3-58	6.6	+
2121 (captive)	14	5-23-58	3.2	—
	17	9- 3-58	2.7	—

^a The plus sign indicates that sperm was present, and the minus sign that it was absent.

increase in weight occurred from November to January (the period of maximum growth rate in juvenile males) in one juvenile male after the removal of one testis in November. After unilateral castration in May the second testis in the remaining adult showed a decrease in weight from May to September, a period when the average weights of testes from wild adults did not differ significantly.

Several captive raccoons were examined repeatedly for sperm in their epididymides after they became sexually mature (Fig. 3). From July through October the greatest percentage of adult males were sexually inactive. The histories of several captives show that individual males had periods that averaged 3-4 months when they were incapable of breeding although males with

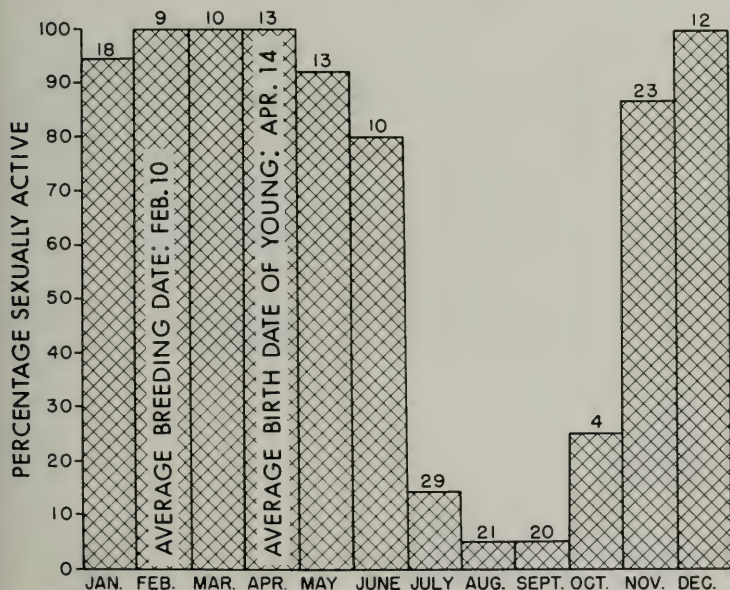


Fig. 3.—Percentage of sexually mature captive male raccoons with sperm in the epididymis. The numeral at the top of each bar indicates the number of observations for each month.

sperm in their epididymides were found in all months (Fig. 3 and 4). Lower concentrations of sperm were found at the beginning and end of the period of sexual activity than were found during

the peak, but how the concentration of sperm is related to a male's fertilizing ability is not known.

Histological examinations of the testes and epididymides of 85 wild and 37 cap-

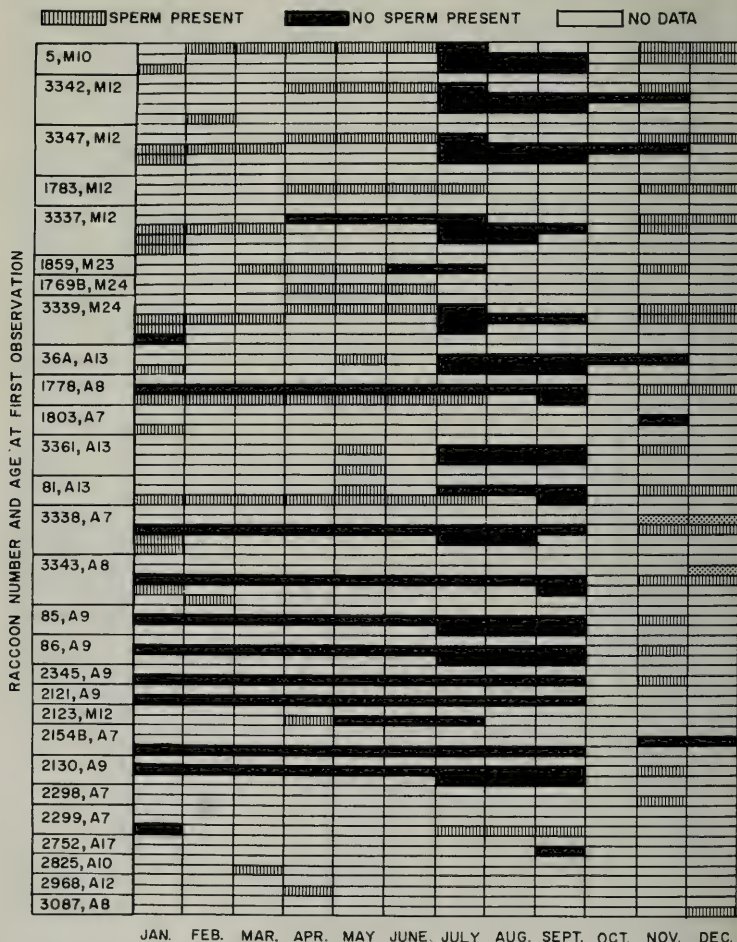


Fig. 4.—Presence or absence of sperm in the epididymides of captive male raccoons. These raccoons were held in outdoor cages throughout the year in Urbana, Ill. The animal's identification number is given first, and the estimated age in months when the first observation was recorded is given next. A = approximate age, M = minimum age. The different lines for each animal indicate different years.

tive male raccoons (Table 3) confirmed the gross observations, reported above, made on captives. In all but five males if sperm were present in the testes, they were also present in the epididymides, and vice versa. Data from these five cases indicate that sperm may be stored in the epididymis for some time after spermatogenesis ceases and that sperm may be found in the testis prior to being stored in the epididymis. Males of some species are able to ejaculate fertile sperm for as long as 4 weeks after castration (Nalbandov 1958: 176). Testes and epididymides removed from two adult raccoons in August (Table 3) are representative of the conditions found. One male had sperm in the seminiferous tubules but none in the epididymides. The second male had low concentrations of sperm in both the testes and the epididymides.

These data show that the male raccoon has a seasonal sexual cycle. The general correlation between the size of the testis and the presence of sperm in the epididymis did not hold in individual cases. Three hundred eighty-four testes with sperm in the corresponding epididymides, taken from adults from October through April, averaged 7.2 grams and ranged from 2.6 to 11.3 grams.

Fifteen testes with no sperm in the corresponding epididymides, taken from adults during the same months, averaged 4.6 grams and ranged from 1.2 to 9.5 grams.

A substantial number of testes were weighed during November, December, and January from the 1950-1951 fur season through the 1960-1961 fur season in Iowa and Illinois. Raccoons in Iowa were examined at a fur house in Bloomfield, Davis County. Most specimens from Illinois were collected at a fur house in Farmington, Fulton County. Farmington is approximately 130 miles, almost due east, from Bloomfield, and the reproductive cycles of the animals collected at these two locations probably were similar. A few Illinois specimens were collected from other fur houses located in the central (north-south) third of Illinois. Each fur buyer bought dead raccoons from hunters and trappers living within a radius of about 100 miles around his location.

These data were collected to study seasonal and annual trends in the weights of testes (Table 4) and the timing of spermatogenesis in relation to age among male raccoons. The testes of juveniles gained weight significantly ($P < 0.02$) from November to January. No signifi-

Table 3.—Occurrence of sperm in the testes and epididymides of adult and juvenile raccoons as determined by histological examination of 85 wild and 37 captive males.^a

Month	Adults ^b		Juveniles ^b	
	Percent with Sperm	Number of Observations	Percent with Sperm	Number of Observations
January	67	3	...	0
February	100	3	0	1
March	100	1	25	4
April	75	4 ^c	57	7
May	25	4	0	2
June	0	1	0	6
July	17	12	0	8
August	25	4 ^c	0	10
September	33	9	0	7
October	80	10	0	8 ^d
November	86	7 ^d	14	7
December	100	1	0	3 ^d

^a All observations were made in Illinois from 1957 through 1960.

^b An adult was more than 12 months of age; a juvenile was 0-12 months of age.

^c One adult male in April and one in August had sperm in the epididymides but not in the testes.

^d One adult male in November and one juvenile male in October and one in December had sperm in the testes but not in the epididymides.

Table 4.—Average testis weights in adult and juvenile raccoons for November, December, and January from the 1950-1951 through the 1960-1961 seasons.

State and Season	Average Weights of One Testis in Grams							
	Juveniles			Adults				
	November	December	January	Average	November	December	January	Average
Iowa ^a								
1950-1951		1.05 (28) ^b	0.73 (3)	1.02 (31) ^c	...	7.99 (23)	6.83 (3)	7.86 (26)
1951-1952	1.12 (66)	1.37 (87)	...	1.21 (153) ^d	7.25 (26)	7.72 (56)	...	7.57 (82)
1952-1953	1.24 (50)	1.68 (4)	...	1.29 (54)	7.35 (14)	7.95 (2)	...	7.42 (68)
1953-1954	0.86 (32)	1.01 (15)	1.10 (2)	0.92 (49) ^e	6.94 (25)	7.94 (11)	8.70 (1)	7.28 (37)
1954-1955	2.04 (32)	2.51 (30)	4.65 (2)	2.34 (64)	7.14 (8)	8.03 (16)	7.50 (2)	7.72 (26)
Illinois ^a								
1955-1956	1.95 (34)	1.59 (19)	2.17 (22)	1.92 (75)	7.13 (3)	5.25 (2)	6.91 (22)	6.81 (27)
1956-1957	1.67 (47)	2.25 (105)	2.72 (24)	2.16 (176)	7.19 (10)	7.22 (46)	7.37 (31)	7.27 (87)
1957-1958	1.99 (52)	2.17 (35)	3.29 (23)	2.32 (110)	6.77 (25)	8.43 (12)	6.25 (8)	7.12 (45)
1958-1959	1.81 (67)	2.41 (62)	3.95 (27)	2.42 (156) ^d	6.93 (27)	6.80 (19)	6.78 (22)	6.84 (68)
1959-1960	1.26 (32)	2.20 (129)	1.00 (3)	1.99 (164)	7.84 (11)	7.18 (47)	5.80 (6)	7.16 (64)
1960-1961	1.47 (95) ^f	1.63 (46)	3.70 (19)	1.78 (160)	6.30 (49)	5.96 (29)	4.87 (26)	5.85 (104) ^d
Monthly average ^g	1.54 (507) ^d	1.96 (560)	2.71 (125)		6.90 (198)	7.34 (263)	6.89 (121)	
Grand average ^g				1.86 (1,192)				7.10 (582)

^a All raccoons were collected at a fur house in Bloomfield, Davis County.^b The numbers of observations are in parentheses.^c Significantly different from the grand average ($P < 0.01$).^d Significantly different from the grand average ($P < 0.05$).^e Most raccoons were collected at a fur house in Farmington, Fulton County.^f Averages not joined by lines are significantly different from each other ($P < 0.05$).

cant differences in the average weights of adult testes occurred from November to January. This finding was not unexpected, because virtually all adult males were capable of breeding by November but only 8 percent of the juveniles had sperm in the epididymides during November (Table 1). There were some statistically significant annual differences in the weights of testes, but the meanings of these differences were not clear.

Females

The ovaries of raccoons showed a nearly steady rate of growth from birth in April through the following November (Table 5 and Fig. 5). In contrast, the testes of juveniles showed their most rapid increases in weight between December and February (Fig. 1).

The ovaries of juveniles reached their maximum average weight in November, approximately 3 months prior to the peak

of the breeding season. The heaviest normal ovaries encountered were found during November in juveniles; the average weights are shown in Table 5 and Fig. 5 and 6. In October, November, and December the ovaries of juveniles weighed more than the ovaries of parous raccoons. The average weights of ovaries for the two groups of females in January were practically identical (Fig. 5).

The ovaries of juvenile (nulliparous) females showed a significant decline in average weight from November through January, and perhaps through March, but the sample sizes for February, March, and April were too small to be definitive. The small sample of juveniles for these latter 3 months resulted partly from classifying raccoons as nulliparous (juveniles) or as parous or pregnant. During those 3 months many females approximately 1 year of age were either pregnant or parous, and hence their ovaries were placed

Table 5.—Average weights of ovaries by month in the raccoon.^a

Month	Nulliparous			Parous or Pregnant		
	Average Total Weight of Both Ovaries in Milligrams	Standard Error	Range	Average Total Weight of Both Ovaries in Milligrams	Standard Error	Range
April (at birth)	4.2 (2) ^b	0.0	4.2- 4.2	282 (3)	31	249-344
May ^c	10.9 (3)	0.4	10.4- 11.8	217 (4)	50	164-259
June	51 (3)	16	20 - 72	224 (2)	43	181-266
July	121 (6)	24	45 -222	171 (7)	30	93-327
August	118 (7)	14	82 -180	198 (4)	42	76-260
September	184 (14)	23	66 -386	217 (3)	27	164-256
October	253 (14)	25	147 -524	227 (4)	25	163-295
November	312 (195)	9	59 -970	271 (80)	12	102-613
December	295 (186)	13	78 -699	229 (81)	10	82-555
January	239 (45)	15	100 -452	244 (25)	23	92-655
February	189 (3)	54	112 -294	275 (5)	41	132-381
March	124 (1)			246 (5)	57	74-382
April	260 (1)					
May ^d	167 (1)					
August	270 (1)					
September	149 (2)	70	78 -219			
November	367 (2)	70	225 -410			
December	233 (12)	27	119 -313			
January	261 (3)	43	204 -346			
March	136 (1)					

^a All raccoons were collected in Illinois, July 18, 1958 through April 18, 1961.

^b The numbers of observations are in parentheses.

^c Most nulliparous juvenile raccoons are approximately 1 month old in May.

^d Most nulliparous adult raccoons are approximately 13 months old in May.

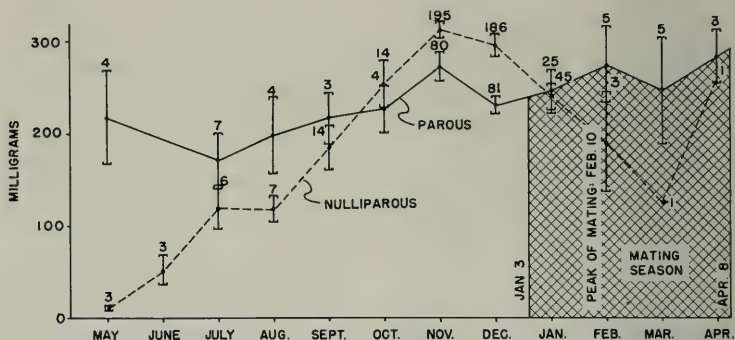


Fig. 5.—Seasonal variations in the average total weight of both ovaries from parous or pregnant and nulliparous raccoons. With each mean are the number of observations and a vertical line representing the mean plus or minus one standard error. All animals were taken in Illinois from July 18, 1958 through May 30, 1961. The data are given in Table 5.

with the adult group. Hence, nulliparous females probably represented only females that did not reach sexual maturity at approximately 1 year of age. All females less than 1 year of age in the January sample were counted as juveniles, as no pregnant female was found during that month.

The seasonal weights of the ovaries in parous raccoons (Table 5) followed a pattern similar to that found for the gonads of adult males (Table 1). The minimum average weight was reached during July, with a slow but consistent increase in weight during August, September, and October. The fall peak

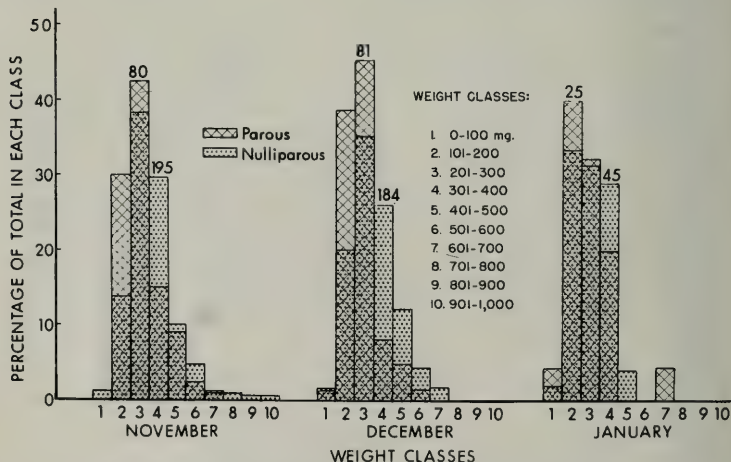


Fig. 6.—The average total weights of both ovaries from parous or pregnant and nulliparous raccoons. All animals were taken in Illinois from November 1958 through January 1961. The numerals at the tops of the bars indicate the numbers of animals in the parous or pregnant and nulliparous groups.

Table 6.—Average total weights of both ovaries in parous and nulliparous raccoons for November, December, and January of the 1958-1959 through the 1960-1961 seasons.^a

Season	Average Total Weight of Both Ovaries in Milligrams						
	Parous			Nulliparous			
	November	December	January	Average	November	December	January
1958-1959	350(15) ^b	270(15)	307(9)	309(39) ^c	355(61) ^d	315(45)	247(20)
1959-1960	219(13)	216(50)	193(2)	216(65) ^c	276(40)	297(110)	246(5)
1960-1961	261(52)	233(16)	211(14)	247(82)	302(99)	252(43)	234(23)
Monthly average ^e	271(80)	229(81)	244(25)		312(200) ^d	295(198)	239(48)
Grand average ^e				249(186)			
							296(446)

^a All raccoons were from Illinois.^b The numbers of observations are in parentheses.^c Significantly different from the grand average ($P \leq 0.01$).^d Significantly different from the grand average ($P \leq 0.05$).^e Averages not joined by lines are significantly different from each other ($P < 0.05$).

weight was reached in November. The ovaries of parous raccoons declined significantly ($P < 0.01$) in average weight from November to December but again increased in weight during January. By April the ovaries of parous raccoons had reached their peak average weight for the year, slightly heavier than in November. The average weight of adults' ovaries in April was a little more than 1.6 times their average weight in July, in contrast to the approximately 2.8-fold increase in average weight reported for the testis in the adult between the low average of July and the high of December.

From the study of ovaries collected during all months and seasons, we gained the impression that differences in weight existed from month to month and year to year. For example, the total weight of both ovaries of parous females averaged nearly 350 mg in November 1958 but only 219 mg in November 1959 (Table 6). Ovaries from nulliparous females killed in November 1958 also weighed considerably more on the average than did ovaries from nulliparous females killed in November 1959. Less striking variations were noted for other months and years. There were also annual differences in the average weights of ovaries from parous females but no significant differences in those from nulliparous females.

MEAN BIRTH DATE OF LITTERS

Wood (1955:409-410) concluded that 7 of the 16 females he examined in Texas had mated by the end of February, but the earliest pregnancy he recorded was March 18. George & Stitt (1951:218) found three litters that were born during March 1950 in Michigan after an unseasonably warm January. Berard (1952:248) observed a lactating female in West Virginia that he estimated had given birth no earlier than August 15, whereas normal births in that area usually occur before May 15. Dorney (1953:123) weighed young raccoons taken in Wisconsin from November 25 through December 22, 1950 and concluded that

Table 7.—Months of birth of raccoons in the northern half of Illinois as determined by actual births or as estimated from examination of embryos.^a

Month	Number of Litters Conceived in Captivity That Were Born in Month Designated	Number of Adult Wild Females Examined for Pregnancy ^b	Number of Litters Conceived in the Wild That Had Actual or Potential Birth Date in Month Designated ^c
January	0	202	0
February	0	6	0
March	2	15	5
April	5	18	12
May	3	9	1
June	1	6	2
July	0	11	0
August	0	4	0

^a All embryos were examined between April 2, 1957 and June 24, 1961.^b Many nonpregnant, adult females examined from April to August were lactating.^c Potential birth dates were estimated (Fig. 8).

"a sizable percentage" of the young had been born later than usual in that year. He suggested that the cold spring weather in 1950 had decreased raccoon mobility and thus had decreased the normal number of early conceptions. A similar situation, discussed later, apparently occurred in Illinois during the breeding season in 1960.

The reports cited emphasize the variation in birth dates that is normal in the raccoon. Most raccoons in the northern half of Illinois are born during April (Table 7). The mean date of birth for 20 litters conceived in the wild, 7 of which were born in captivity, was April 18; the earliest date of birth was March 9, and the latest, June 24. The potential birth dates of embryos measured in dead

females were estimated by measuring uterine swellings (Table 8 and Fig. 7).

The mean date of birth for 11 litters conceived and born in captivity in Urbana, Ill., was April 24. The monthly distribution of these births is shown in Table 7. The earliest date of birth for a litter conceived in captivity was March 16; the latest was June 3.

Although 202 wild females were examined for pregnancy during January and 21 were examined during February, July, and August (Table 7), only one pregnant female was observed during these 4 months. When examined on February 25, she appeared to be due to give birth in about 3 weeks.

ESTIMATING BIRTH DATES OF RACCOONS

Table 8.—Estimated number of days prior to birth based on the measurement of uterine swellings in captive raccoons.

Largest Measurement of Uterine Swellings in Millimeters	Days Prior to Birth
8	55
20	39
25	35
30	33
35	33
40	30
45	23
55	17
110	1

Uterine swellings were measured to the nearest millimeter and the dates of birth were recorded for eight litters believed to have been born at full term (Table 8). (One litter was measured on two occasions.) Because it was difficult to measure accurately the crown-rump length of embryos, especially during the early stages of pregnancy, the measurement recorded was the greatest measurement of the external uterine swelling. In the early stages the swellings were essentially round, and the measurement was greater than the crown-rump measurement, of

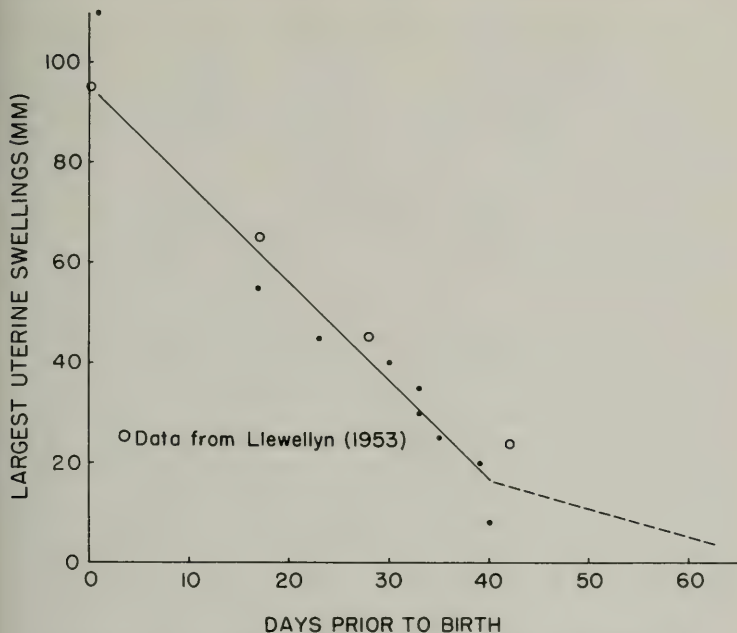


Fig. 7.—Sizes of uterine swellings in raccoons at various numbers of days prepartum. The line was fitted by least squares, not including Llewellyn's data. The dash line, an extension of the line to conception 63 days prepartum, is not based on data. The size used for the uterine swelling at conception was 5 mm, the approximate average diameter of the uterus during estrus. The data are given in Table 8.

the embryo. In the later stages the swellings were elongate and the measurement approximated that of the crown-rump measurement.

The dates of mating were not known, but it was possible to graph the size of the uterine swellings in relation to the number of days prior to parturition (Fig. 7). The line was fitted by least squares and gave a good fit for uterine swellings between 20 and 60 mm in size. When we used this line to estimate the dates of birth for eight litters, the maximum error was 4 days when the uterine swellings were between 20 and 60 mm. In one litter uterine swellings larger than 60 mm were measured and in another litter uterine swellings smaller than 20 mm were measured. Measure-

ments of the swellings in these two litters appear to indicate slower-than-average growth from conception to the 20-mm size and faster-than-average growth from the 60-mm size to birth. Measurements of uterine swellings made during this study were similar to those reported by Llewellyn (1953:321). Our data and Llewellyn's make it possible to estimate the date of birth (Fig. 7). If we assume a gestation period of 63 days, which many authors agree is average for the raccoon, it is possible also to estimate the date of conception.

SECONDARY SEX RATIOS

Incidental information collected during the present study indicated that the sex

Table 9.—Secondary sex ratios in raccoons.^a

Sex of Embryos and of Young at Birth ^b			Sex of Wild Litters Less Than 2 Months of Age		
Females	Males	Percent Males	Females	Males	Percent Males
47	36	43 ^c	21	33	61 ^c
	$\chi^2=1.46$ ($P<0.25$)			$\chi^2=2.67$ ($P<0.10$)	

^a All were from Illinois, taken during the breeding seasons of 1957 through 1961.

^b Includes young conceived in the wild and born in captivity as well as young conceived in captivity.

^c Neither group is significantly different from 50:50 ($P \geq 0.05$); however, the ratios of the two groups may be different from each other ($P < 0.06$).

ratio of raccoon embryos and of young at birth, combined, and the sex ratio of young raccoons less than 2 months old were not significantly different from 50:50 (Table 9). There were more males ($P<0.06$) among the young less than 2 months old than among the embryos and young at birth, indicating some differential mortality of females between birth and 2 months of age. Other investigators have examined limited numbers of young raccoons at birth or prior to 2 months of age to determine secondary sex ratios. Stains (1956:31) reported that the sex ratio was approximately 1:1 at birth in the raccoon, as shown by counts of litters. Stuewer (1943a:213; 1943b:68) counted all of the young in eight litters ranging in age from 7 to 60 days and found 14 males and 19 females (42 percent males).

ESTROUS CYCLE, OVULATION, AND PSEUDOPREGNANCY

Estrous Cycle

Published reports regarding the estrous cycle in the raccoon do not agree. The raccoon has been reported to have one heat period and one breeding season each year (U.S. Department of Agriculture 1936). Stuewer (1943a:212) found that occasionally an adult female failed to mate successfully in spring and then bred later, but that yearling females either mated during the regular breeding season or did not mate until the next breeding season. Asdell (1946:135) reported: "In New England mating begins in the last week of January and there

may be a later season for young females . . ." Whitney & Underwood (1952:83) stated that, on the basis of actual observations under normal conditions, the period of mating in the raccoon was from January until March; if this period was missed, another normal period of 2 months' duration occurred 4 months later. During his studies of raccoons in Texas, Wood (1955:409) found Graafian follicles in the ovaries of one female examined in April and thus concluded that breeding can occur as late as April. Because ovulation normally occurred early in the year, this finding suggested to him that raccoons were possibly polyestrous.

Observations made on captive raccoons held in outdoor cages in Urbana, Ill., confirmed Stuewer's (1943a:212) observations on the absence of delayed breeding in yearling females. General observations made on several captive, yearling females showed that either they became pregnant or pseudopregnant at the time when adults became pregnant, or they did not breed until the next breeding season. These observations were confirmed by examining the ovaries of two yearling females several times from March through August. Their ovaries and uteri remained small and inactive during the entire period. Thus, we believe that delayed breeding in yearling females does not contribute substantially to the number of litters born later in the year than usual.

Dates of ovulation were estimated by observing birth dates and by direct examination of Graafian follicles, corpora lutea, and embryos. Heat and ovulation probably occurred at about the same time.

Table 10.—Approximate number of days between ovulations in five captive raccoons.

Estimated Date of First Ovulation	Estimated Date of Second Ovulation	Days Between Ovulations	Remarks
2-10	5-10	89	During first pregnancy, carried embryos half way or more to term but resorbed them.
Before 3-14	5-26	70 ^a	Pseudopregnant
Before 3-10	5-11	62 ^a	Pseudopregnant
3-2 (± 2)	6-23 (± 2)	84	Pseudopregnant
1-29	6-16	141 ^b	Carried embryos to term each time. Young of first pregnancy all dead 4 days postpartum.

^a Minimum.^b The interval between the births of two litters in one season.

On the basis of our observations of five captive raccoons for which the approximate dates of the first and second ovulations were known (Table 10), we found that the interval between ovulations in captive raccoons in Urbana, Ill., varied approximately from 80 to 140 days—and not invariably 4 months, as reported by Whitney & Underwood (1952:83). The shorter intervals that we observed agree with Millard's (1939:28-29) data. He obtained two litters in one breeding season from 6 of 10 captive raccoons in Wisconsin whose young were removed on the day of birth and whose mates were returned 3 days later. Seven of the females were observed to mate 10-16 days after the young were born. If we assume a gestation period of 63 days and that the female raccoon ovulates on the day of mating, ovulations in Millard's animals occurred 73-79 days apart.

Under normal circumstances wild, adult female raccoons in Illinois rarely skip a breeding season. Special circumstances may interfere with the regular breeding cycle, causing a higher-than-normal percentage of the litters to be born late (Dorney 1953:123). Such interference occurred in some sections during the 1960 breeding season in Illinois. Temperatures at the Urbana and Peoria weather stations (U.S. Weather Bureau 1960) were average for January 1960, but mean temperatures in February were 15.7° F [9.0° C] below normal. Snowfall at Urbana and Peoria for February and March 1960 ranged from 8 to 16 inches [20.3-40.6 cm] per month higher than

the average for the preceding 10 years. On the Allerton Park Study Area (Piatt County, east-central Illinois) young raccoons were caught in live traps beginning in early June of each year from 1957 through 1961, with the exception of 1960. In 1960 the first young were live-trapped after September 1 even though trapping was conducted during the entire summer.

Eyes were collected from 257 juvenile raccoons killed by hunters and trappers over a wide area centered around Farmington in west-central Illinois during the 1960-1961 hunting season. The lens technique (Sanderson 1961b:482-485) was used to estimate birth dates. The lenses indicated that the peak of births in 1960 occurred in mid-April, the usual time, but that a second, smaller peak occurred at the first of July, about 11 weeks later. These two peaks were separated by about the length of one estrous cycle, as it was estimated from our observations of captive raccoons. According to the lens data, approximately 16 percent of the young were born during August, September, and October in 1960—later than the latest date of birth reported in Table 7—indicating that under some circumstances a substantial number of wild raccoons have had more than one estrous cycle in a year.

In view of Millard's (1939:28-29) success in getting two litters in one season from captive raccoons and because the present study demonstrated that some of our captive pseudopregnant and pregnant females had second heat periods in captivity, it was, at first, surprising that so

few second litters were conceived in captivity during our study. Millard's (1939) objective was to rear a large number of young raccoons for restocking purposes, and no doubt he disturbed his animals as little as possible. Our study, on the other hand, required frequent handling of the animals and their subjection to laparotomies. Only two pregnancies are known to have resulted from second ovulations during our study. The first female became pseudopregnant after her first ovulation, and the single embryo from her second ovulation was resorbed; the second female gave birth to her second litter in August, 141 days after the first litter was born. She had killed the last surviving young of her first litter 4 days postpartum.

Female raccoons will not ovulate and come into estrus so long as they are nursing young. Young were removed at birth from four female raccoons and 5 days after birth from one female. All of these females were returned to their mates when the young were removed, but no second matings were observed and no second pregnancies resulted. Young were removed from six females at periods varying from 17 days to 6 weeks after birth, and the males were returned to the females. One female was given a drug that caused her to abort or resorb her young. Her mate remained with her at all times. However, no second pregnancies resulted in any of these animals. In addition to these females several others underwent periods of pseudopregnancy during the normal breeding season while remaining with their mates through the summer. No late pregnancies resulted. Possibly some of the males were no longer capable of fertilization (Fig. 3 and 4) by the time their mates experienced their second estrous cycles.

Our data make it clear that in Illinois it is possible for raccoons to ovulate two times during one season and even to give birth to two litters. However, to give birth to the second litter, the female must lose her first litter on or shortly after the day of birth. We have no evidence that

ovulations occur after lactation ceases in the raccoon. In any case, it appears that raccoons must nurse for 2-3 months in the wild and that probably they usually nurse for 3-5 months (Stuewer 1943a: 213; Montgomery 1969:155-158).

The vaginal smear is frequently used to determine the stage of the reproductive cycle in the laboratory mouse, rat, and guinea pig. Stockard (1932:1612-1627) gives a general review. Although this technique can theoretically be applied to other species, many problems occur with species that have relatively long periods of proestrus and estrus. Nalbandov (1958:103-104) pointed out that all mammalian females show changes in their vaginal histology during the estrous cycle. He further reports:

"The vaginal-smear technique is most useful, however, with animals having short estrous cycles . . . ; in animals with longer cycles . . . vaginal changes lag from one to several days behind ovarian changes, and vaginal smears are therefore less reliable indicators of ovarian events."

Stuewer (1943b:64) observed that from 1 to 2 weeks elapsed from the onset of vaginal swelling in the raccoon until the female would receive the male. After a receptive period of about 3 days, 3 or 4 weeks elapsed before the vulva returned to normal appearance. Whitney & Underwood (1952:83) reported that the onset of the mating cycle could be recognized by a thickening or swelling of the vagina and vulva and traces of bloody fluid (absent in some females), and that the female would accept the male at the onset of the mating cycle and was receptive for a period of 3-6 days.

We obtained estrous-type vaginal smears for a period of several weeks in our raccoons; examples of these smears are shown in Fig. 8. An estrous-type smear was obtained from a castrated female 36 days after the end of treatment with estradiol and progesterone (Fig. 8B). One captive female must have mated during the 7 days between the taking of two vaginal smears; she gave birth

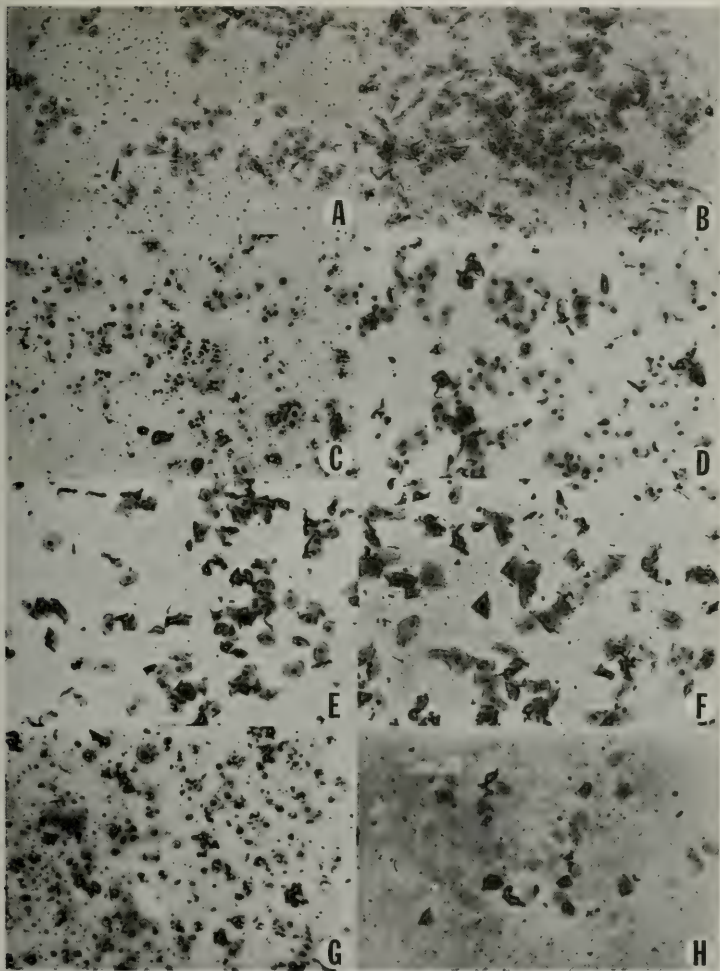
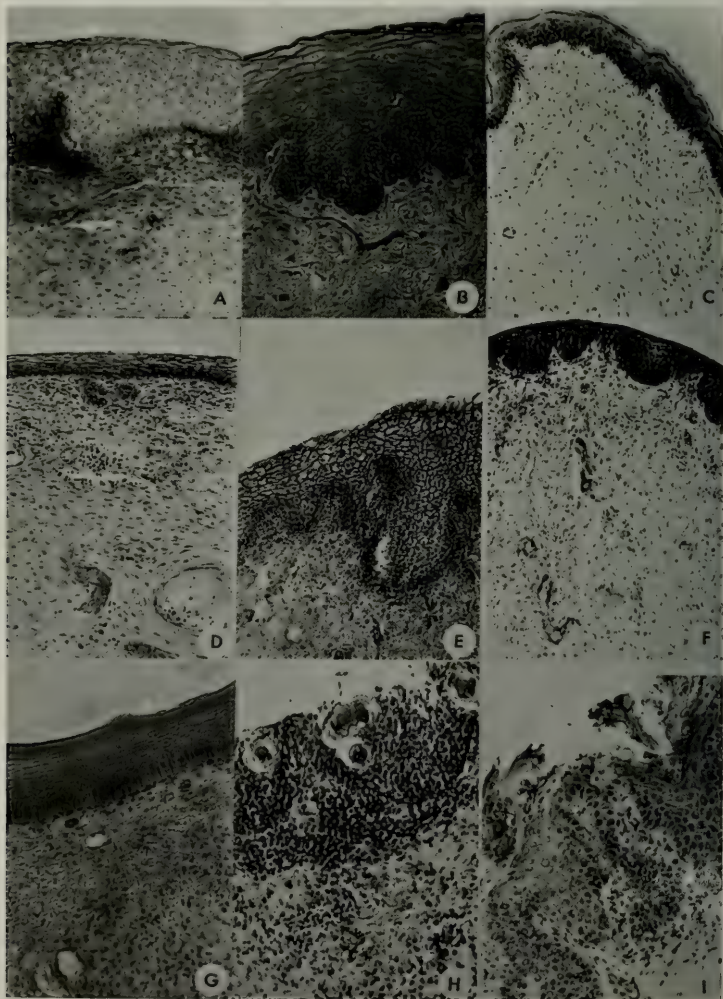


Fig. 8.—Vaginal smears from captive raccoons representing various stages of the estrous cycle. A, female 1292; ovaries removed May 14, 1958; smear taken July 23, 1959. B, castrated female 1297; second ovary removed August 13, 1957; smear taken May 16, 1958, 36 days after treatment with estradiol and progesterone ended. C, nulliparous female 2525; smear taken December 4, 1958. D, female 2959; smear taken January 11, 1958. E, female 2959; smear taken March 7, 1958. F, female 2959; smear taken March 14, 1958; female 2959 must have mated between these two dates, because she gave birth to young on May 13, 1958. G, adult female 1786; smear taken April 12, 1957. H, female 2114; smear taken February 21, 1958; uterine swellings were 8 mm in diameter. The smears were stained with Wright's blood stain and are shown 62 times actual size.

60 days after the second smear was taken (Fig. 8E and F). On the basis of the results obtained from this study, we conclude that the days when a female raccoon will receive a male can not be identified by examination of vaginal

smears. The vaginal smear appeared to be no more specific than gross vulval swelling—which can be observed much more readily. Leucocytes (Fig. 8C and G) were seen in vaginal smears from raccoons only infrequently. The paucity of



vaginal smears containing leucocytes suggested that the raccoon may pass through metestrus in a relatively short time.

Many of the difficulties inherent in using vaginal smears may be avoided by taking vaginal tissue for biopsies—a simple procedure in the raccoon. Samples of vaginal tissues were removed from both anesthetized and unanesthetized animals (Fig. 9). However, vaginal tissues from castrated females (Fig. 9A and B) showed that the histology of the vaginal epithelium is not a reliable indicator of estrus in the raccoon.

Ovulation

Whitney & Underwood (1952:84), without citing evidence, reported that in the raccoon "sufficient stimulation is produced during copulation to insure ovulation." Llewellyn & Enders (1954a: 440) removed one ovary from each of four sexually mature raccoons that had been isolated from males before and during the normal breeding season. They found "well developed follicles" in each ovary but no corpora lutea and, on the basis of this evidence, suggested that ovulation in the raccoon is not spontaneous but is induced by copulation.

In our study one female was approximately 5 months old when captured about 5 months before the breeding season. She was isolated for 3 months prior to the breeding season. Her nipples were moderately stimulated but unpigmented when a laparotomy was first performed on her 3 months after she was isolated. The ovaries were each 8 X 5 mm—small for ovaries with corpora lutea—yet each

ovary had two corpora lutea, each 5 mm in diameter. Thirty-five days later the corpora lutea were essentially unchanged in size and appearance. Sixty days after the first examination the ovaries were 10 X 5 mm, and the corpora lutea were slightly paler and were between 3 and 4 mm in diameter. Ninety-three days after the initial observation no traces of the corpora lutea were visible.

A second female that was isolated was approximately 40 days old when captured. She was isolated 2 months prior to the breeding season, and the first laparotomy was performed on her 2 months after the isolation began. Her nipples were only slightly stimulated, and her ovaries, measuring 8 X 4 mm, contained no corpora lutea. The left ovary had one clear follicle and the right ovary had two, each follicle measuring 2 mm in diameter.

Nine days later the right ovary had four freshly ovulated follicles, each 3 mm in diameter. The left ovary had a single follicle of the same size with a tiny hole in its highest point. It was believed that this female had ovulated no more than 2 days earlier.

Twenty-six days after the freshly ovulated follicles were observed, the right ovary was 11 X 5 mm and had three corpora lutea, each 4 mm in diameter. Either the fourth follicle in the ovary did not form a corpus luteum, or it was obscured by one of the other corpora. The left ovary was 10 X 5 mm and had one corpus luteum of the same size as those in the right ovary.

Eighty-one days after the freshly ovu-

Fig. 9 (Page 52).—Photomicrographs of vaginal biopsies from captive raccoons representing various stages of the estrous cycle. A, female 1292; ovaries removed May 14, 1958; biopsy performed July 23, 1959. B, castrated female 1297; second ovary removed August 13, 1957; biopsy performed May 16, 1958, 36 days after treatment with estradiol and progesterone ended. C, female 2114; biopsy performed February 21, 1958; uterine swellings 8 mm in diameter. D, nulliparous female 2525; biopsy performed December 4, 1958. E, female 1297; biopsy performed July 23, 1959; no treatment with estradiol and progesterone after April 3, 1958. F, female 1298; biopsy performed October 5, 1959; ovulated about September 24, 1959 as a result of injections of pregnant mare's serum. G, female 1782; biopsy performed October 29, 1957; treated with estradiol beginning October 17, 1957; ovaries removed June 10, 1957. H, female 2959; biopsy performed January 27, 1960; ovulated after December 18, 1959 as a result of treatment with follicle-stimulating hormone and luteinizing hormone; corpora lutea present. I, female 2805; biopsy performed February 24, 1960; fresh corpora lutea present. The sections were stained with hematoxylin and eosin and are shown 122 times actual size.

lated follicles were observed, the ovaries were each 8 X 3 mm; the four corpora lutea, each now 3 mm in diameter, were still present. By 102 days after the corpora were first seen, four whitish corpora albicantia (not examined histologically), each measuring 1 mm in diameter, had formed at the sites of the preceding corpora lutea. At this time there were also two follicles, each 2 mm in diameter, in the right ovary and one of similar size in the left ovary. The female was judged ready to ovulate a second time.

Thirty-one days later one corpus luteum was found in the left ovary and five or more were found in the right ovary; each corpus luteum was approximately 5 mm in diameter. The left ovary was removed (133 mg) and sectioned, but no ovum was found in the corpus luteum. Thus, this animal had probably ovulated. Also, the secretory material in the endometrial glands indicated that progesterone had been secreted. Seventy-three days after the follicles were examined, the corpora lutea were still present but measured only 2 mm in diameter.

A female found when approximately 3 weeks old was kept as a house pet until the middle of April, when she was about 1 year of age. At that time she suddenly became vicious, severely biting both owners. She remained the most vicious raccoon we have seen among the many dozens of wild, captive, and pet raccoons that we have handled. According to her owners, she had never come into contact with other raccoons. At the time her behavior changed, her nipples were moderately stimulated and moderately pigmented, indicating that she was either pregnant or pseudopregnant. When first examined, her ovaries were 9 X 6 mm and 7 X 5 mm, respectively, and contained a total of five corpora lutea, each 3 mm in diameter. The size of the corpora indicated that they were regressing when examined, because newly formed corpora lutea in the ovaries of raccoons are approximately 5 mm in diameter. Thirty-five days after the initial examination all five corpora lutea were plainly visible but were regressing and were

slightly smaller than when first examined. Forty-eight days later (83 days after the first examination) no traces of the corpora lutea could be seen by gross examination.

The data on these three isolated females, one of which ovulated twice in one season, show that the raccoon is a spontaneous ovulator, and refute Llewellyn & Enders' (1954a:440) interpretation of their observations. The statement of Whitney & Underwood (1952:84) that ovulation in the raccoon is dependent upon copulation is not true for captive raccoons in Illinois.

In many captive raccoons, especially those reared as pets, the onset of estrus and pseudopregnancy was apparent from changes in behavior. A docile house pet sometimes suddenly became vicious and unmanageable. In all such cases that we examined, corpora lutea were present in the ovaries. The formation of corpora lutea was invariably accompanied by changes in the uteri and nipples whether the animal was pregnant or only pseudopregnant. The nipples always enlarged, and some became heavily pigmented, some became only slightly pigmented, and still others remained unpigmented. With the onset of pseudopregnancy the uteri became turgid and opaque and were considerably enlarged from their size during anestrus; however, they were not fluid filled and somewhat *rubbery*, as they were during estrus.

A female raccoon born in April was reared as a pet until the following January, when she became too unruly for the owners to handle and was donated to our project. She is described here as representative of the females, housed with other raccoons, that ovulated but did not become pregnant. According to her owners, she had not come into contact with other raccoons before she was donated to our project. Two days after we received her, she was placed in a cage with four yearling males. Forty-nine days later her nipples were tiny and white, but after 21 more days (March 28) they were elongated and black, indicating that she was either pregnant or pseudopreg-

nant. Five days later her left ovary was removed, and histological examination showed four freshly formed corpora lutea.

Histological examinations of the ovaries from this nonisolated female, from one isolated female, from three nonpregnant wild females, and from two additional nonisolated, nonpregnant, captive females revealed no ova in the corpora lutea. No substantial difference was noted between the corpora lutea of the isolated nonpregnant and of the nonisolated nonpregnant females. Ovaries from several nonpregnant females housed with other females, or with males, were examined during and after the breeding season. In several cases these ovaries had corpora lutea, which were grossly identical to those seen in females isolated prior to the breeding season and to corpora lutea in pregnant females. Thus, we concluded that corpora lutea in both isolated pseudopregnant and nonisolated pseudopregnant females formed from ovulated follicles and not from luteinization of follicles. Normal-appearing corpora lutea were also formed in the ovaries of a female in which ovulation was induced by exogenous hormones.

Data gathered from examination of 13 captive raccoons indicated that corpora lutea persist in pregnant females until parturition. Observations on four of these captives indicated that corpora lutea disappeared 14–16 days after parturition if the young were taken from the mother within 5 days after birth. In one of these four the corpora lutea were not present 16 days after parturition; in another they were present 14 days after parturition.

One female ovulated, apparently for the second time in the season, about May 11. She mated, and one embryo was implanted; approximately 20 days after ovulation the embryo was dead. Traces of one corpus luteum were still present in each ovary approximately 52 days after ovulation, and, on the basis of size and appearance, we concluded that they undoubtedly persisted for a maximum of 60 days.

In five nursing females the corpora lutea disappeared before the ovaries were examined from 11 to 35 days postpartum. A sixth female examined 11 days after parturition had four regressing corpora lutea, each 3 mm in diameter, in her left ovary and none in the right ovary. The corpora were those observed when she was first examined 34 days before the birth of her young. She was examined again 20 days after giving birth, when only four corpora albicantia were present in her left ovary. Thus, in this nursing female, the corpora lutea disappeared between 11 and 20 days after parturition. Corpora lutea were not found in histological preparations of ovaries from two wild, lactating females, nor by gross examination of the ovaries from six other wild, lactating females.

Pseudopregnancy

Our data indicate that corpora lutea persisted for about the same length of time in captive pseudopregnant raccoons as they did in those that give birth to young. Corpora were present 61 days but not 82 days after the estimated date of ovulation in one pseudopregnant captive. Three other pseudopregnant females showed similar periods of pseudopregnancy, although the data for these females were less precise than were the data for the first. The persistence of corpora in females that went at least halfway to term did not appear to differ significantly whether the young were aborted, were resorbed, or were born and were removed at birth or nursed until weaned. In one female, discussed in the preceding section, the young were resorbed at an early stage and the corpora lutea disappeared no more than 60 days after ovulation.

In some species pseudopregnancy may equal normal pregnancy in duration, but in most animals it lasts about half as long (Nalbandov 1958:218). Our observations indicated that all captive raccoons that ovulated, but did not become pregnant, underwent a period of pseudopregnancy much as does the dog. In the raccoon pseudopregnancy lasted ap-

proximately the same length of time as does normal pregnancy and followed ovulation.

Our observations of wild female raccoons during the breeding season indicated the relative incidence of pregnancies and pseudopregnancies, and supplied substantiating evidence that corpora lutea disappear in wild, lactating females, as in captives, shortly after they have given birth. Histological sections were made of ovaries collected from March through June (1957 through 1961) from 15 wild females 2 years of age or older. Six were pregnant, four were pseudopregnant, and five had recently given birth. Corpora albicantia were present in the ovaries of four of the five parous females, and corpora lutea were present in all of the pregnant and pseudopregnant animals. The fifth parous female, collected March 1, had recently given birth or aborted, as indicated by the fresh placental scars in her enlarged uterus and the four corpora lutea in her ovaries; however, she was not lactating. Corpora lutea were not found in histological sections of the ovaries from 39 young-of-the-year, 14 *yearling* (12–20 months old), and 10 adult wild raccoons collected from July through January.

Of 15 wild, parous female raccoons collected from February through September, only 1 had freshly ovulated follicles in February, and another had corpora lutea in March. None of the remaining 13 females, including 6 that were lactating, had corpora lutea. As mentioned earlier, histological examinations of ovaries from lactating, captive females indicated that corpora lutea disappear between 11 and 20 days after parturition, regardless of whether the females nurse their young.

From February through June (1957 through 1961) we made 30 observations on 24 captive female raccoons 2 years of age or older. Five were caught only a few days prior to examination. Of the 30 observations, 18 were of pregnant animals, 8 were of pseudopregnant females, and 4 were of animals neither pregnant nor pseudopregnant when examined. The

one animal that accounted for two of the four latter observations had an abnormally large uterus but inactive ovaries in 1959. Her uterus was enlarged but her ovaries were small when she was examined in May of 1957. Thus, she did not represent the norm. The other two observations of females that were neither pregnant nor pseudopregnant were of adult females that had given birth to litters in previous years; each was examined once during subsequent mating seasons. Because each was examined only once during the breeding season of the year in which corpora lutea were not found, it is conceivable that they had undergone pseudopregnancy but that the corpora had regressed before they were examined. Thus, evidence from both captive and wild females indicated that a majority of the females 2 years of age or older were either pregnant or pseudopregnant each year.

Every year during the hunting and trapping season a small percentage of females, judged to have ovulated on the basis of the stimulated or pigmented nipples, or both, were without uterine placental scars. During the fur seasons in Illinois from 1956–1957 through 1960–1961, uteri were examined from 284 females that appeared, on this basis, to have ovulated, and 7 (2.5 percent) had no placental scars. The evidence indicated that these animals had been only pseudopregnant. Some annual variation occurs in this characteristic. During the 1960–1961 fur season, all 77 females judged, upon examination of their nipples, to have ovulated had placental scars in their uteri.

PERCENTAGE OF YEARLING FEMALES THAT WERE SEXUALLY MATURE

Of 21 captive female raccoons approximately 1 year of age examined from February through June, 11 were either pregnant or pseudopregnant, but 10 were sexually immature. Histological sections of the ovaries from nine wild yearlings collected from February through August showed no corpora lutea in the five non-

pregnant females nor in the two lactating females, but corpora were present in the ovaries of the two pregnant yearlings. Gross examination of the ovaries from five wild, nulliparous yearlings collected from March through August showed that the ovaries of four contained no corpora lutea, but that three corpora lutea were present in one female collected in May. Thus, 10 of 21 captive yearlings and 9 of 14 wild yearlings were sexually immature.

During two fur seasons in Illinois (1959-1960 and 1960-1961) nulliparous adults with tiny unpigmented nipples accounted for 15 of 164 (9.2 percent) adult female raccoons examined. These nulliparous adults, with tiny unpigmented mammae, probably did not ovulate during the first breeding season after their birth.

SECRETION OF PROGESTERONE BY CORPORA LUTEA

The period of the production of progesterone by corpora lutea in the raccoon is unknown, but circumstantial evidence indicates that corpora lutea probably secrete progesterone as long as they are present (discussed later in connection with the production of uterine milk). One female had five corpora lutea, each 5 mm in diameter, when first examined on April 10. At that time we traumatized her left uterine horn by inserting a needle into the uterine lumen two times, each time scratching the entire length of the inside of the uterine horn with the point of the needle as it was withdrawn. Eight days later the ovaries and corpora were unchanged in gross size and appearance. The left uterine horn showed no evidence of trauma, but there is no direct evidence that the uterus of the raccoon will respond to traumatization with a decidual reaction in the presence of progesterone.

PIGMENTATION OF MAMMAE

Several female raccoons were studied to establish a possible physiological cause for the pigmentation or nonpigmentation

of nipples. Some pseudopregnant yearling females developed heavily pigmented nipples, whereas others did not. The presence or absence of pigment was not correlated with nursing, abortion, resorption of embryos, age at first estrus, or any other factors we could recognize. Unpigmented nipples remained so throughout life, but lightly pigmented nipples sometimes became darker with age. The pigment was not sloughed after nursing as Snyder & Christian (1960:650) found in the woodchuck (*Marmota monax*).

INTERSTITIAL TISSUE

Many studies were conducted before 1920 on the interstitial tissue in mammalian ovaries. Interstitial tissue is present in greater or lesser amounts in the ovaries of some species and is apparently absent in others. Little is known about its function. His (1865) was apparently the first to describe interstitial tissue cells in mammalian ovaries and to discuss their importance. Allen (1904: 120, 141) concluded that interstitial cells were formed from connective tissue during a process of degeneration in both the testis and ovary, and noted many points of similarity between the cells of the interstitial tissue and the lutein cells of corpora lutea. Kingsbury (1914:86) discussed the interstitial cells in the domestic cat (*Felis catus*) and recognized the lipid nature of the granules in these cells, but he found no evidence that the cells constitute morphologically an intra-ovarian gland. He also reported their presence in immature, newly born, and fetal kittens.

Rasmussen (1918:395) believed that in the woodchuck the interstitial cells proliferated from the terminal epithelium during adult life. He found a marked seasonal variation in the number of interstitial cells and in the amount of lipid present in them in the woodchuck. These cells gradually increased in number during hibernation and hypertrophied rapidly immediately after hibernation (Rasmussen 1918:371-372). Maximum numbers were seen in females that did not

become pregnant until late in the breeding season. Retrogression began with pregnancy and the growth of corpora lutea and continued until July. The ovarian interstitial cells were minimal in size in late summer and early autumn but then began to enlarge. After an extensive review of the literature, Rasmussen concluded, in accord with the vast majority of the investigators, that the interstitial cells come either directly from the connective tissue (stroma) of the ovary, or indirectly from the theca interna of atretic follicles.

According to Corner (1932:1597), the stroma of the rabbit ovary consists so largely of epithelioid cells heavily laden with lipid granules that the entire organ is a solid mass of interstitial cells in which the follicles and corpora lutea are embedded. This finding led to the concept that the ovarian stroma in this and similar species was a gland of internal secretion, the so-called interstitial gland. Embryological study showed that interstitial cells were largely derived from the theca interna of atretic follicles and that interstitial cells were found in many species at a very early stage of embryonic differentiation, in which case they seemed to be produced by the modification of the cells of the stroma and of the various epithelial proliferations. The pig ovary (Corner 1932:1597) contains epithelioid cells only in follicles and corpora lutea, the stroma cells being simply fibroblasts. Corner (1932: 1597) reported that the cat ovary was between the extremes represented by the rabbit and pig ovaries. In the adult human ovary there appeared to be epithelioid cells only in follicles and corpora lutea.

It is conceivable that interstitial cells, whether found in great numbers in the stroma of the rabbit or in thin layers in atretic follicles in humans, are functionally the same, but proof is lacking (Corner 1932:1597). Corner (1932:1598) further reported that in all of the species he studied the interstitial cells contained granules of neutral fat or, at least, of lipoids, which reduce osmic acid and stain with Sudan III. Some workers are

ready to assume that the lipoids found in the interstitial cells represent a true internal secretion.

Much of the older work, mentioned by Stafford & Mossman (1945:97), showed that in some mammals the development of ovarian interstitial tissue is at its maximum during proestrus and estrus and that all of the animals included in this group, most of which breed annually or semiannually, have long reproductive cycles. The literature reports no evidence of ovarian interstitial tissue in laboratory rodents, which have short estrous cycles, and there is no easily discernible cycle in the amount or state of interstitial tissue that could be correlated with pregnancy in the guinea pig. There is a trend toward a maximum amount of interstitial tissue in the cortex near estrus and into early pregnancy and a minimum in midpregnancy. The high and low in the medulla seemed to occur a week or two later than in the cortex, suggesting that in the guinea pig medullary interstitial tissue originates from that of the cortex.

Patzelt (1955) studied the interstitial tissue in several carnivores and emphasized that age, time of year, and stage of the reproductive cycle greatly affected the interstitial cells. He also pointed out that other investigators considered thecal cells, which are traced back to the particularly active atresia of follicles during pregnancy, to be closely associated with the cells of the corpora lutea. Thus, Altmann (1927) thought it conceivable that only a topographical contrast existed between thecal granulosa and lutein cells.

Patzelt (1955) regarded the interstitial tissue cells as producers of hormones and as a storage place for the substance necessary for the formation of new follicles and for propagation in general. The basis for his ideas was the fact that the lipid-containing cells are variously derived within the rudimentary ovary from germ layers, thecal cells, and cells of the surrounding stroma, and that it is not possible to demarcate the source of the interstitial cells. He usually found that ovarian interstitial cells were filled with

stored lipoids after a heat period and during pregnancy. After parturition a decrease in stored lipoids occurred that led to a functional dimorphism simultaneously with the formation and maturation of new follicles.

Hansson (1947) concluded that the abundance of interstitial tissue in the mink (*Mustela vison*) indicated that the tissue performed a special task. Because anestrus in the mink lasts from May to January, when no follicular growth beyond the vesicular stage takes place, the interstitial tissue may serve as a regulator during this time, governing sexual differentiation.

A preliminary study of the abundance of interstitial tissue in histological sections of the ovaries of 119 raccoons taken in all months indicated that interstitial tissue cells were abundant at some stages of the reproductive cycle, often occupying as much as 50–90 percent of the space in the ovary. However, interstitial tissue cells were seldom abundant when corpora lutea were present. Of 21 pairs of ovaries with corpora lutea, only 3 had significant amounts of interstitial tissue. One of these is shown in Fig. 10G.

Females less than about 2 months of age did not have large amounts of interstitial tissue in their ovaries. With this exception the ovaries of females less than 12 months old contained more, both relatively and absolutely, of this tissue, on the average, than did the ovaries of older females.

Seasonal trends in the abundance of interstitial tissue were apparent in ovaries with no corpora lutea. The ovaries removed from 16 adults from January through June contained little interstitial tissue. Ovaries removed from 26 adults killed from July through December contained more interstitial tissue than did those collected earlier in the year. No trend was apparent in the amount of interstitial tissue within the July–December period. During this interval ovaries from adults did not contain as much interstitial tissue as did ovaries from females less than 12 months old.

Ovaries from raccoons less than 12

months of age showed less seasonal variation in the abundance of interstitial tissue than did the ovaries from older animals. Small amounts of interstitial tissue were present in ovaries removed from seven juveniles in May and June, when most young were less than 2 months old. The ovaries excised from 24 juveniles in July, August, and September contained more interstitial tissue than did the ovaries examined in May and June, but the differences among the amounts of interstitial tissue found in July, August, and September were slight. The greatest abundance of interstitial tissue was discovered in 16 pairs of ovaries taken from juveniles during October and November. The maximum ovary weights recorded during this study were those of juvenile females in November (Table 5). Nine pairs of ovaries were examined from females not yet 1 year old killed during the period December through April. The abundance of interstitial tissue in these ovaries did not appear to differ from that in the ovaries of juveniles examined from July through September.

In spite of marked seasonal and age differences in the abundance of interstitial tissue, there was no apparent correlation between its abundance and the size or amount of coiling of the uterine glands. The development of the uterine glands and the presence of secretory material in these glands were largely dependent upon the presence of corpora lutea.

Three sources of interstitial tissue have been suggested, germ layers, thecal cells, and cells of the surrounding stroma, and all three may be present in the raccoon. Small amounts of interstitial tissue were present in some raccoon ovaries at birth. Judging from appearance alone, we believe it probable that some interstitial tissue in the raccoon is formed from degenerating follicles. Several cases similar to the one shown in Fig. 10A were seen during this study. In other ovaries there appeared to be a *streaming* of the cells as the interstitial tissue formed, presumably from the germinal epithelium

One striking feature of interstitial cells, although the luteal cells were generally larger (Fig. 10). Under the microscope was their resemblance to luteal cells,



these two kinds of cells appeared more alike than the photographs in Fig. 10 indicate.

PLACENTAL SCARS

Deanesly (1935:464) first reported that she could recognize parous uteri in the stoat (*Mustela erminea*) by the presence of pigment granules that later workers called *placental scars*. Deno (1937: 433, 445) found that placental scars were produced in the mouse by accumulations of hemosiderin in the cells of the reticulo-endothelial system and that the placental scars were associated with the involuting metrial gland. Deno (1941) later reported that placental scars were visible in both the rat and mouse for a year or longer. Conaway (1955:516-517) stated:

"The placental scars of the rat appear as yellow to black pigmented areas along the utero-mesometrial border. Their origin seems identical with that of the scars in the mouse In both the rat and mouse, the metrial gland is a prominent structure at the base of the placenta Presumably it is formed by an extension of the decidual response into the connective tissue of the myometrium. The pigment-laden cells are concentrated in this area between the longitudinal and circular muscle layers although some are found in the deeper stroma of the endometrium. As the age of the scar increases the pigmented area may decrease in size and appear darker in color."

Sooter (1946:69-70) counted placental scars to determine the numbers of young produced by muskrats (*Ondatra*

zibethicus) although no critical work has been done to determine whether the number of placental scars corresponds to the number of young born. Elder (1952) reported the failure of placental scars to reveal breeding history in captive mink. Brambell & Mills (1948:241), working with the European rabbit (*Oryctolagus cuniculus*), again pointed out

"that although there is little likelihood of failure to detect implantation sites containing living embryos the possibility remains of the disappearance before full term of sites in which the embryos had died and were reabsorbed soon after implantation or, more probably, that such sites might be overlooked, through becoming less conspicuous, and hence omitted from the counts."

In laboratory rats and wild brown rats placental scars were only a crude indication of the number of young produced (Davis & Emlen 1948: 166), with errors as high as 100 percent in either direction. Conaway (1955:531) found that placental scars in the laboratory rat were always formed if all embryos were resorbed after the 11th day of pregnancy, whereas total resorption prior to this time never caused the formation of scars. If some of the embryos were resorbed, death on the seventh day or later resulted in scar formation at all resorption and term sites. If some embryos were resorbed between the 8th and 11th days and the remainder after that, scars were formed at all sites. The size and appearance of resorption scars were similar to those of term scars. Momberg & Conaway (1956: 379) found that 32 of 312 placental scars from previous pregnancies were overlapped by scars of second pregnan-

Fig. 10 (Page 60).—Photomicrographs of luteal and interstitial cells of raccoons, showing similarities in the two. A, female 2137; luteal cells (X 94); ovary removed March 19, 1958; pregnant. B, female 1292; luteal cells (X 94); ovary removed May 14, 1958; ovulation caused by injections of pregnant mare's serum. C, female 2805; luteal cells (X 94); ovary removed February 24, 1960; fresh corpora lutea resulted from natural ovulations; pseudopregnant. D, female 2232; interstitial cells (X 94); ovary removed August 7, 1958; wild animal approximately 3 months old. E, female 2403; interstitial cells (X 94); ovary removed November 6, 1958; wild animal 7 months old. F, female 2234; interstitial cells (X 94); ovary removed August 8, 1958; wild animal 3 months old. G, female 1292; luteal cells (X 375); ovary removed May 14, 1958; ovulation caused by injections of pregnant mare's serum. H, female 2242; interstitial cells (X 375); ovary removed August 27, 1958; wild animal 4 months old. The sections were stained with hematoxylin and eosin.

cies in the white rat. They could not always recognize the superposed scars by gross examination, but microscopic recognition was possible.

The placenta of the raccoon was first described by Watson (1881:280-296). The zonary placenta of the raccoon is similar to that of other carnivorous mammals. Watson (1881:279) noted:

"The placenta formed a complete ring, but at the centre of its widest part, *i.e.*, opposite the back of the foetus, there was a spot similar to that figured by Daubenton in the placenta of *Martes domestica*, and described by Bischoff in that of *Lutra vulgaris*, *Mustela foinea* and *Mustela martes*, where the substance of the placenta was deficient. This deficiency involved the entire thickness of the placenta, so that a probe could be passed from the uterine to the chorionic surface of the organ without injury to its substance."

The placenta of *Procyon* is truly deciduous in character, as it is in the dog, cat, fox, and seal. According to the classification of Mossman (1937:224), the raccoon placenta is endotheliochorial. Placental scars in the raccoon were apparently first noted by Stuewer (1943b:68), who autopsied a female raccoon in May and found four placental scars in the uterus; he believed they indicated that four young had been born. Sanderson (1950:399) examined uteri from six captive females and concluded that "placental scars may be an accurate measure of litter size in raccoons."

If placental scars are to be useful in estimating the reproductive performance of a species, several facts about them must first be known. Pertinent questions are: (1) Is one placental scar formed for each implantation site regardless of the fate of the developing embryo? (2) If the answer to the first question is no, then what stages of embryonic development result in the formation of placental scars? (3) Is it possible to differentiate placental scars formed from embryos that go to term from those formed from embryos that are aborted or resorbed? (4)

How long do the placental scars persist, and is the length of time they persist affected by the female's subsequent breeding history? (5) Are the placental scars recognizable at all seasons of the year? (6) If the placental scars persist beyond a subsequent pregnancy, is it possible to recognize scars representing litters from different years? Some preliminary information on all of these questions has been obtained.

In only 2 of 27 litters with a total of 98 embryos in 2 of 20 captive female raccoons that we examined did we find discrepancies between the number of embryos observed and the number of placental scars identified later. One female (No. 2960) had four embryos, estimated to be 30 days of age when examined on May 26, but five grossly identical placental scars when the uterus was removed 6 months later. The additional scar may have represented a litter of one from a previous year. If so, the scar was overlooked when this same uterus was examined during the fall before the four embryos were observed. The extra scar may have also represented an additional embryo that was aborted or resorbed prior to the time the four embryos were examined. The second female (No. 4022) had two live and one dead embryo when first examined on February 19. She gave birth to two live young 29 days later, but when her uterus was examined 11 days after parturition, there were two grossly identical scars in each horn. There were four corpora lutea in her left ovary and none in the right. Thus, the additional scar observed at the second laparotomy was probably from an embryo that was aborted or resorbed prior to the first examination.

A captive female raccoon (No. 2960) had four embryos, estimated to be 30 days of age, when examined. She was given a drug, Malucidin, that caused either abortion or resorption. The embryos were gone 13 days later, and the sites of attachment were indicated by large bumps. When the uterus was removed 6 months later, five placental scars were identified by slight bumps. We

split the uterine horns and identified the five placental scars as typical for captive females. (Possible differences in placental scars of captive and wild animals are discussed below.) Thus, in this female, one placental scar was formed for each of the four embryos even though all four embryos were either aborted or resorbed at midterm. As has been discussed, the fifth scar either persisted from the previous year or resulted from an embryo resorbed prior to the first examination when the four embryos were about 30 days of age.

Another captive female raccoon (No. 3333) had four live embryos and one that was being resorbed in her uterus on March 21. It was estimated that the embryo being resorbed had died 30 days after conception. The young were born 33 days after the initial examination. Sixteen days after the birth of the litter the placental scar representing the resorbed embryo was smaller than the others, but 47 days after parturition no gross difference could be detected among the five scars.

One pregnant captive female raccoon (No. 2824) was castrated approximately 50 days prepartum, but her embryos continued to grow for about 20 days before they were aborted and resorbed. A second captive pregnant female (No. 2151) was castrated approximately 30 days prepartum, and her young were aborted about 1 week prepartum. Two months after abortion or resorption the placental scars in these females could not be differentiated grossly from those formed by normal embryos born at term. Female No. 2824 was killed 4.5 months after she was castrated. When she was killed, only one placental scar was found, both before and after the uterus was split, even though the exact locations of the embryos were known. The one scar was dark and broad, and appeared to be typical of those formed from young born during the current breeding season. The scar was formed at the site of one of three embryos present 19 days after castration. All three of the embryos were aborted prior to 26 days after castration.

The data from the two castrated females (No. 2824 and 2151) that lost their young and from six intact captive females that resorbed or aborted some or all of their embryos indicated that one placental scar was formed for each embryo that existed for approximately 30 days, whether or not any embryo went to term.

We have made some observations on the persistence of placental scars in the raccoon (Table 11). Placental scars were present, although indistinct, in one female (No. 2959) when her uterus was removed nearly 19 months after her young were born. Scars were visible 12 and 17 months after parturition in another female (No. 1786), but could not be seen in her enlarged uterus stimulated by hormones 14 and 24 months after parturition. Her ovaries were removed approximately 1 year after the birth of her young, and, after castration, she was treated with estradiol and progesterone at various intervals. These treatments may have affected the rate of disappearance of her scars. A third female (No. 2779) had placental scars for 14 months, but not 23 months, after

Table 11. — Persistence of placental scars in captive raccoons.

Raccoon Number	Number of Months Scars Persisted After Parturition	
	Minimum	Maximum
19	4.0	...
1782	5.0	...
1786	17.0 ^a	30.0
2120	6.0	...
2124	4.5	18.5
2124	8.0	...
2125	16.5 ^b	...
2151	3.0	...
2184B	15.0	27.0
2230	6.0	...
2779	14.0	23.0
2959	18.5	...
2960	19.0	30.0
3333	14.0	...
3350	3.5	...

^a Not visible macroscopically — approximately 14 months after parturition — in the uterus stimulated by hormones.

^b Not visible macroscopically during the subsequent estrus, approximately 10 months after parturition, but the same scars were again visible macroscopically 16.5 months after parturition.

parturition, and a fourth female (No. 2125) retained placental scars nearly 17 months after parturition. None of these females gave birth in the second year.

There was no macroscopic evidence of placental scars from a 1958 litter (Female 2124) 18.5 months postpartum, but histological examination revealed a few scattered pigment granules, and scars from a 1959 litter were prominent. Thus, the 1958 scars disappeared, for practical purposes, prior to 18.5 months after parturition, when she had a litter the following year. All female raccoons had placental scars when examined from 2 to 10 months after the birth of their young. The evidence indicated that if a female failed to give birth to a litter in the next year, placental scars persisted for approximately 19 months in captives, but not as long as 24 months. If a captive gave birth to a litter the next year, scars from the first litter persisted for 10 or more months but not as long as 19 months.

One captive raccoon became pregnant at the second ovulation during one season. The single embryo, in the process of being resorbed when it was first observed, was estimated to be 20 days old. Twenty-one days later the site of placental attachment was readily identified as a bump 8 X 7 mm in size; 61 days after the initial observation no trace of the scar could be seen. Thus, this scar disappeared between 21 and 61 days after the resorbing, 20-day embryo was observed. The absence of living embryos in this captive may have been an important factor in the rapid disappearance of the scar.

The variability in the length of time that placental scars were visible in the raccoon after parturition is shown in Table 11. In two females scars were not grossly visible in their stimulated uteri during or near estrous cycles of the ensuing years, because their enlarged uteri caused a diffusion of the pigment granules of the scars, making them invisible. Scars in these females were again visible macroscopically when the uteri regressed.

Scars from a litter born in May 1958 (discussed above) could not be seen (No. 2124, Table 11) 18.5 months later (December 1959) even though their exact locations were known and the uterus was removed and split. After we sectioned the site of one scar, we were able to identify a few scattered pigment granules in the endometrium. Two scars from a litter born in April 1959 were easily identified macroscopically in this same uterus 8 months (December 1959) after the birth. In a second female (No. 2959, Table 11) scars from young born in May were not visible with translucent light after the uterus, which was stimulated, was removed 18.5 months later. All four scars from this litter were located and were identified by the slight bumps visible at the placental sites. After the uterus was opened, all four scars were visible as pale, brownish areas, but they might have been overlooked had not their exact locations been known. When one of these scars was examined histologically, moderate numbers of pigment granules were seen in clumps and scattered in the endometrium and in the adjacent myometrium.

The distribution of pigment granules in the uteri of two wild females was studied in histological sections. Each of these females had four scars at autopsy. Pigment granules in the uterus of one female were somewhat scattered but seemed to concentrate in a ring deep in the endometrium near the myometrium. Many pigment granules were scattered throughout the endometrium of the uterus of the other female.

Pale placental scars were often difficult to see *in situ* in a live animal, and early in the study some scars may have been overlooked. We believe that, after we became experienced in looking for scars, no visible placental scar was overlooked, but they could not be seen in pregnant females and females at or near estrus. When the scars had practically disappeared, they could be observed only by splitting the uterus. Thus, these pale scars would be overlooked when examining live females by laparotomy. If the

uterus of a live female was stimulated, many of the placental sites could best be identified by slight, opaque bumps rather than by the pigmentation. Identification of the location of scars by the presence of bumps was possible for several weeks after parturition, when the uterus was still stimulated, as well as in the stimulated uterus at or near estrus. After the uterus regressed, scars were usually readily visible as bumps or could be identified by using translucent light to observe the pigmented areas. The pigmented areas could also be located when the uterus was opened or by histological examination.

Placental scars seem to persist longer in wild raccoons than they do in captives. The placental scars of captives that we examined from October through January after the births of their litters were generally pale brown, small, and slightly opaque. A majority of the wild females examined during these same months had larger, more opaque scars, often black. Many (55.2 percent in 1959 and 41.0 percent in 1960) uteri of wild, parous females had more than one group of scars, which differed in size and density (Fig. 11). Presumably these scars were from different years; however, some might have been from different litters born in 1 year. There was no evidence that as many as 40 or 50 percent of the wild females gave birth to second litters during a single season. Thus, placental scars probably persist for 20 months or

longer in many — perhaps in all — wild females. In the few wild females with three groups of scars, the first group may have persisted for as long as 32 months.

The placental scars of raccoons are useful for estimating litter size and rate of productivity. However, these scars must be used with caution, and care must be taken to separate properly the groups of scars. We do not know for certain the significance of multiple groups of scars. We can say with reasonable confidence that each embryo that reaches 1 month of age is represented by one scar for 10 or more months. Scars in wild females with only one group of scars probably reflect implantation rates for the preceding breeding season. Most single groups of placental scars occur in females that have mated successfully only once.

MORPHOLOGY OF THE REPRODUCTIVE TRACTS

Males

The duct system and accessory glands in the reproductive system of the male raccoon (Fig. 12) are similar to those found in the dog, as described and shown by Nalbandov (1958: 42–44). Seminal vesicles are lacking, as they are in the dog, fox (*Vulpes fulva*), and wolf (*Canis lupus*). The Cowper's glands (bulbo-urethral glands) are also absent. The walls of the vasa deferentia thicken prior to entering the prostate and form the ampullae. The ampullae and the urethra



Fig. 11.—Raccoon uterus (X 0.75) split to show two groups of placental scars. This female was killed on January 23. Two light scars were only barely visible in the photograph but were readily visible in the fresh specimen. Their locations and densities relative to the three dark scars are indicated by the light stippling (arrows).

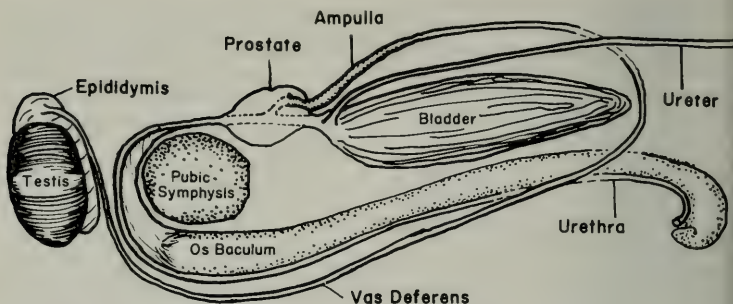


Fig. 12.—Schematic drawing (side view) of the reproductive system (X 0.85) of an adult male raccoon.

unite inside the prostate to form a common duct. The many compartments of the prostate gland open into this duct system.

The *os penis* or *os baculum* (bone of the penis) is well developed in the raccoon. Its stage of development has been used to separate males into two age groups (Sanderson 1950: 395-396; 1961a: 11-14). The os baculum was once used by tailors as a ripping tool for taking out basting threads (Jaeger 1947: 297).

We found several raccoon bacula that had been broken and then healed. Sanderson (1950: Plate 11) showed a photograph of some of these bones. Our data from wild males shed some light on possible causes for these broken bones. During four hunting and trapping seasons in Illinois (1957-1958 through 1960-1961), 7,233 bacula from juvenile raccoons were examined. Forty-three (0.6 percent) of these had been broken but were healed or healing, and 238 (3.3 percent) were freshly broken. At the same time, 4,152 bacula from adults were examined. Eighty-six (2.1 percent) of these had been broken but were healed, whereas 41 (1.0 percent) were freshly broken.

These data indicate that most of the breaks in the os baculum of the raccoon occur in juveniles. The bacula of juveniles are much softer and more easily broken than are those of adults. Hunters often shake a raccoon out of a tree and

let their dogs fight it. Fighting with dogs could account for the freshly broken bones found in both adults and juveniles, and the more durable bones of adults would explain the smaller percentage of freshly broken bacula found in older raccoons.

Females

The raccoon uterus (Fig. 13) is somewhat intermediate between the bicornuate uterus found in the pig and insectivores, and the bipartite uterus found in the cat and dog. There is a single cervix and the horns are distinct, but after the horns join externally to form the single, small uterine body, the uterine lumina remain separate — even though this separation is not apparent from the outside — to a point near the cervix.

Llewellyn & Enders (1954b: 439) removed one ovary, ovarian capsule, oviduct, and proximal end of the uterine horn in each of two raccoons. After closing the cut ends of the uteri with sutures, they released the females. When retrapped the next year, each female was carrying three embryos, two each in the normal horns and one each in the ovariectomized horns. Thus, even though the internal separation of the uterus extends nearly to the cervix, ova can pass from one uterine horn to the other. In our study some indirect evidence of transuterine migration of ova was noted. In a few cases more embryos were found

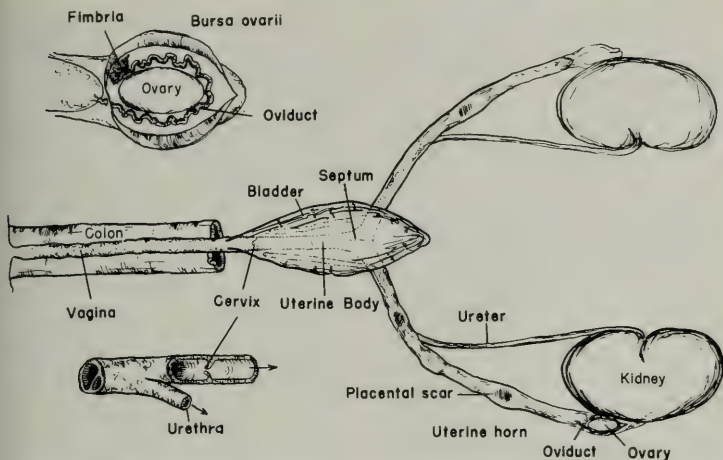


Fig. 13.—Schematic drawing (ventral view) of the reproductive tract (X 0.5) of a parous female raccoon.

in a uterine horn than there were corpora lutea in the corresponding ovary, but the total number of corpora lutea present in both ovaries was usually the same as the number of embryos or placental scars present in both uterine horns.

The ovary in the raccoon, ovoid in shape, is completely surrounded by the bursa ovarii (Fig. 13). This sac is intact except for a small slit on one side, not large enough to permit passage of the ovary as in the mink (*Mustela vison*), dog, and fox. One of our captive females had a congenital deficiency of the bursa that was large enough to permit passage of the right ovary. This opening was slightly dorsal to the normal slit in the bursa but was not connected with it. The left ovarian bursa was normal. This captive was the only such animal among several hundred examined. Watson (1881: 273-274) observed one raccoon and reported that the ovary was destitute of any peritoneal pouch or pavilion such as formed an almost complete sac in many animals.

The fimbria is extensive, and in the estrous female the edge of the fimbria is bright red and protrudes through the

slit in the capsule. This bit of fimbria grossly resembles the gills of a fish. The fimbria joins with the end of the oviduct. The oviduct is highly convoluted and makes an almost complete circle around the ovary before entering the uterus (Fig. 13).

Two, three, and sometimes four ova were observed in a single follicle. When an ovary contained one follicle with multiple ova, several other follicles with multiple ova were usually present.

Approximately 25 female raccoons from Iowa and approximately 25 from Illinois were examined for the presence of the *os clitoridis*. A bone — 11 mm in length — was found in only one clitoris. Rinker (1944: 91) found four ossa clitoridae in four female raccoons examined in Kansas, but found no bones in the clitoria of four other females from a "distant locality," apparently in Kansas. Burt (1960: 8) used Rinker's observation as the basis for stating that the *os clitoridis* is present in the raccoon. Sanderson (1950: 398) found only one *os clitoridis* among 100 female raccoons in Missouri. Because only a small percentage of females examined from Mis-

souri, Iowa, and Illinois had ossa clitoridæ, there may be geographic variation in the presence of this bone. Its presence is not of general occurrence in raccoons in all localities.

EFFECTS OF CASTRATION

Males

Some effects of castration on the development of the os baculum in the raccoon have been discussed by Sanderson (1961a: 13-14). The information in that report, with additional observations, is presented here. The lack of sex hormones in males was reflected by the much shorter and thinner bacula in castrated animals in comparison with bacula from intact animals of similar ages (Sanderson 1961a: Fig. 4). The lack of sex hormones became apparent at 8-11 months of age in castrated males. Sanderson (1950: 396) showed that in intact males the penis normally became extrusible at about 10 months of age, but a castrate male (Sanderson 1961a: Fig. 6, No. 59) had a nonextrusible penis and a small baculum at 22 months of age. This baculum was only slightly longer and heavier than one from a castrate raccoon only 10 months of age (Sanderson 1961a: Fig. 5, No. 209), but both were much shorter and thinner than were the bacula from intact males 18-23 months of age (Sanderson 1961a: Fig. 6). The baculum from the castrated raccoon 22 months of age was dense like an adult bone and not spongy at the base as were bacula of similar size from raccoons 12 months of age and younger.

Thus, we concluded that the level of sex hormones affected the enlargement of the preputial orifice and maturation of the penis bone but had little or no effect on the development of the baculum prior to 7 months of age.

Castration in males also apparently caused a slight delay in the closure of the epiphyseal cartilage in the radius and ulna, but because most of the castrated males in this study died of disease at early ages, not enough information was available to demonstrate this relationship conclusively.

Epiphyseal plates were classified as closed (without cartilage), thin (intermediate condition), or broad (with a thick plate of cartilage) (Sanderson 1961a: 7). One castrated male had broad epiphyses at 17 months of age and thin epiphyses at 20 months of age. His epiphyses were still thin when he died at 22 months of age. When examined, 35 intact males with broad epiphyses were 15 months of age or less, whereas 14 of 17 males (82 percent) with thin epiphyses were 13-19 months of age. Epiphyseal plates in 11 of 13 intact males closed between 16 and 21 months of age (Sanderson 1961a: 16). The effects of castration on epiphyseal closure merit further study.

Females

The time of closure of epiphyses in females was much like that in males, but the greater variation in the upper ages of females with thin epiphyses indicated that epiphyseal closure was delayed in some females or occurred later in some than in others.

One factor that perhaps influences age at epiphyseal closure is the level of circulating hormones. Two females were castrated to study the effects of the absence of ovarian hormones on epiphyseal closure. One female, born in the wild, was castrated at an estimated age of 4 months, and one, born in captivity, was 3 months old when castrated. The first had broad epiphyses at 14 months of age, thin epiphyses at 20 months of age, and thin epiphyses when she died at 23 months of age. The second had broad epiphyses at 22 months of age, thin epiphyses at 25 months, and nearly closed epiphyses at 27 months of age. Epiphyseal development and closure in these two castrated females were delayed in comparison with the rate of development and closure found in the average intact female. Four additional females were castrated at estimated ages ranging from 13 to 24 months. Our observations suggested that the removal of the ovaries, even after raccoons had reached sexual maturity but before the epiphyses closed, delayed the rate of epiphyseal closure.

Major factors that may have contributed to the variations we observed in age at epiphyseal closure in female raccoons were (1) age at first mating, (2) hormone secretion level, and (3) quality and quantity of nutrition. Factors influencing age at epiphyseal closure should be studied further because the available data are somewhat contradictory.

Thus, our data and those of Sanderson (1961a: 10-11) suggest that epiphyseal closure in the castrated female raccoon is delayed in comparison with that found in the average intact female but falls within the limits of variability for intact females.

In mammals castration after implantation and during the first third or first half of pregnancy usually leads to abortion or resorption of the fetuses (Nalbandov 1958:221). In some mammals the ovaries are required throughout gestation, but other mammals do not lose their young after castration, once the crucial period is past.

Two pregnant females were castrated to learn whether the raccoon is a species in which pregnancy is maintained after castration. To establish limits after which castration is tolerated, these two animals were castrated approximately 11 and 38 days after conception, respectively. (It had been established earlier that performing laparotomies on pregnant raccoons did not interfere with pregnancy.)

The first of these two pregnant female raccoons that we castrated was born in 1959 and reared as a pet. She gave birth to a litter in 1960. On February 5, 1961 she forcibly repelled the approaches of her mate. Twenty-five days later she had three embryos in her left uterine horn and two in the right but only four corpora lutea. Each uterine swelling was 10 mm in diameter. We estimated the embryos to be 11 days old, suggesting that mating had occurred about February 17. Both ovaries were removed on March 2, and 19 days later two embryos in the left uterine horn were being resorbed. These two swellings were almost as large as the other three, but the surfaces were collapsed and flaccid, not turgid like those of a normal swelling. The embryos

were still present at both sites. The remaining three embryos, 45 X 20 mm, looked almost normal, except that the swellings appeared less round and turgid than normal swellings are. We could not discern whether the embryos were alive or dead. We estimated that, if they were alive, they would be born in 25 days (Fig. 7). Thus, these embryos had a normal rate of growth for 19 days after the castration of the female. No embryo was found 26 days after castration. From gross appearances we concluded that the last three embryos were aborted and the first two were resorbed.

Twenty-eight days after this female raccoon was castrated, her mate was returned to her cage. The next day, only 3-10 days after her young were aborted, this pair was observed in copulation. This activity suggests the possibility that postpartum heats, which occur in several species such as the sow and mare, may not be dependent upon the presence of the ovaries.

This female escaped 3 months after she was castrated and was taken in a steel trap 52 days later. After she was killed, it was discovered that she was lactating profusely. When the mammary gland was sliced with a scalpel, the entire cut area immediately filled with milk. She was lactating more than 4.5 months after her ovaries had been removed and 4 months after her young had been resorbed and aborted. However, the second pregnant female that was castrated showed no indication of lactation 5 months after removal of her ovaries.

No traces of ovarian tissue were found during the autopsy performed on the first of these females. The uterus, measuring 7 X 4 mm, was turgid and appeared similar to uteri of animals at estrus, but sectioning showed the endometrium to be devoid of even traces of glands. Other female raccoons, months after being castrated, had thick epithelia lining their vaginas (Fig. 9A), suggesting the possibility of an extraovarian source of estrogen in the castrated female.

The second of the pregnant raccoons that was castrated was placed in captivity in 1958 when she was about 2 months

old. She had two embryos in each uterine horn on February 28, 1961, when both ovaries were removed (approximately 38 days after conception and 25 days before parturition), but the left ovary had three corpora lutea and the right ovary only one corpus luteum. Nineteen days after castration and 6 days prior to expected parturition, one dead embryo weighing 43 grams was found in her nest box. The average birth weight of eight newly born raccoons that we weighed was 61.8 grams. The embryo was well developed but did not have much hair, and its hair was shorter than in most young at birth.

Twenty-one days after castration the uterus contained enlarged areas where the young had been attached. One of these sites was opened and examined. Detritus was present, but there was no other evidence of resorption, which was occasionally seen in both wild and captive females. Thus, all four embryos were probably aborted about 1 week prepartum.

Although the two females were castrated at different stages of pregnancy, the embryos apparently persisted for about the same length of time in each—19 days after castration—33 days short of term for the first female and approximately 7 days short of term for the second.

EFFECTS OF EXOGENOUS HORMONES

Males

Two male raccoons were studied to learn whether injections of androgen would initiate or prolong spermatogenesis during the male's period of summer sterility. The first animal chosen was an adult male at least 20 months old when he was captured. In August (during the period of sexual inactivity) the left testis was removed, weighed (1.6 grams), and preserved for histological study. The average weight of one testis from an adult in August was 2.6 grams (Table 1). Sperm could not be found in the epididymis, but spermatogenesis was occurring in a few seminiferous tubules. This male was given six testosterone doses of 30

mg each subcutaneously over a period of 18 days. He was killed 21 days after the removal of his left testis and the first injection of testosterone. The right testis weighed 1.6 grams, and no sperm were present in either the seminiferous tubules or epididymis.

Histological comparison of the two testes and the epididymides showed slight changes that we attributed to the testosterone injections. Both before and after the hormone treatment most spermatogenic cells were approximately 8 microns, and the nuclei 3 microns, in diameter. However, after testosterone injections a few of the cells were as large as 11 microns in diameter. The lumina of the seminiferous tubules remained about the same size after the treatment as they were before, but after the injections the cells of the seminiferous tubules were more scattered than they were before treatment. Sperm were present in the seminiferous tubules prior to treatment, but not afterwards. Sperm could not be found in either epididymis, one of which was removed and examined before and the other after the hormone treatment. The epithelial lining of the tubules was 46 microns tall prior to treatment and 30 microns after treatment (each height is an average of five measurements), indicating degenerative changes, perhaps caused by the hormone. The average outside diameter of the tubules was 140 microns prior to treatment and 65 microns afterwards.

A second male raccoon, captured when approximately 3 months of age, was reared as a pet. He was approximately 16 months old when his left testis, weighing 3.3 grams, was removed in August. The epididymis contained many motile sperm.

He was treated with four doses of 12 mg each of testosterone over a 13-day period. He was killed 15 days after the removal of the left testis and the first injection of the hormone. At that time his right testis weighed 2.5 grams, and many motile sperm were in the epididymis. Histological examination revealed few changes in the cells of the seminiferous tubules.

A few sperm were present in the seminiferous tubules both before and after treatment. After treatment sperm were not found in a section of the epididymis, but a few were observed in a drop of fluid collected from the tail of the epididymis.

Females

Ovulation can be induced during anesthesia in several species of domestic and laboratory animals by the injection of gonadotrophic hormones. Hammond (1952:218) used pregnant mare's serum (PMS) as a follicle-stimulating agent and chorionic gonadotropin to cause ovulation in ranch mink.

We made several attempts, using 19 individuals, to cause the growth and development of follicles and to cause ovulation in the raccoon by injecting hormones. Only four individuals ovulated, and three of these cases involved the use of PMS (Table 12). Only the four cases in which ovulation occurred are discussed.

In one series of experiments various dosages of follicle-stimulating hormone (FSH) given subcutaneously were followed by luteinizing hormone (LH) given intravenously. Later FSH and LH were mixed and given subcutaneously, followed by intravenous injection of LH. With one exception all attempts using FSH and LH were unsuccessful in causing ovulation. In some cases normal-appearing follicles were numerous in the ovaries after injections of FSH and mixtures of FSH and LH, but attempts with LH and with a mixture of LH and FSH to cause the follicles to ovulate were unsuccessful. The ovaries generally were overstimulated; that is, they were larger than normal and contained more follicles than normal.

The successful ovulation that did not involve injections of PMS occurred in a female raccoon (the first female in Table 12) approximately 44 months old, weighing 6.7 kg. Each ovary was 11 X 6 mm, with no follicles or corpora lutea approximately 2 months prior to the breeding season. A section of her uterus was removed when the ovaries were measured (approximately 2 months prior to the

breeding season) so that we could study the pigment granules. The next day subcutaneous injections of a mixture of 10 Armour units (AU) each of FSH and LH were begun. These injections were given for 10 days, and on the 12th day a mixture of 80 units each of FSH and LH was injected intravenously. At that time each ovary was 12 X 8 mm and contained 10-20 clear follicles, each about 1 mm in diameter. On the 13th day 100 units each of FSH and LH were injected intraperitoneally as a mixture. On the 16th day the left ovary was 18 X 9 mm and contained approximately 20 follicles, each about 2 mm in diameter, but ovulation had not occurred. The left ovary weighed 760 mg, compared with an average weight of about 137 mg for one ovary of parous or pregnant females during the mating season (Table 5). When the raccoon was killed 45 days after the first injection, her right ovary weighed 290 mg and contained 11 corpora lutea.

In a second series of experiments PMS was injected into eight females in attempts to cause the development of follicles and to cause ovulation. Three of these attempts were successful. The first female was approximately 2 years of age and had been in captivity for more than a year when hormone treatments were begun. We injected 100 international units (IU) of PMS subcutaneously each day for 12 days and 500 IU each on the 13th and 16th days. Thirteen days later, 28 days after the treatment was begun, the uterus and both ovaries were removed. The contents of the oviducts and uterine horns were flushed out, but no ova or blastocysts were found. Each ovary contained approximately 30 corpora lutea. Even though no ovum was recovered, the abnormally large number of corpora lutea containing no ova indicates that this female probably ovulated. The secretory material found in the lumina of the uterine glands indicated that progesterone had probably been secreted.

The second female was captured when she was at least 18 months of age; however, she was not injected with hormones until she was about 53 months old. Sub-

Table 12.—Attempts to cause ovulation in raccoons by injections of exogenous hormones.

Estimated Age of the Raccoon in Months ^a	Weight in Kilograms	Injection Date ^b	Dose (each) ^c	Hormone	Laparotomy or Autopsy Date and Results
21	5.80	1-17-58	Successful Ovulations 2.5 mg 200 IU 500 IU	Estradiol ^d PMS ^e PMS	5-6-58: 4 embryos in uterus. 5-13-58: Young born.
		4-16-58-4-28-58 5-1-58			
		12-3-59-12-12-59 12-14-59			
		17-15-59	10 AU ^f 80 AU ^g 100 AU ^h	FSH ^e , LH ^{h,i} FSH, LH FSH, LH	12-14-59: Ovaries 12 x 8 mm; 10-20 follicles 1 mm diam in each ovary.
24	3.18 /	4-16-58-4-27-58 4-28-58, 5-1-58	100 IU 500 IU	PMS PMS	12-18-59: Left ovary 18 x 9 mm, 760 mg; 20 follicles 2 mm diam, not ovulated. 1-17-60: Right ovary 290 mg; 11 corpora lutea.
		9-9-59-9-20-59 9-21-59	100 IU 550 IU ^j	PMS PMS	5-14-58: 60 corpora lutea.
53	4.76				9-21-59: Many unovulated fol- licles. 9-24-59: Approx. 12 <i>blut</i> <i>punkte</i> in each ovary. Left ova- ry 826 mg; 26 early-stage cor- pora lutea. 10-5-59: Right ovary 2,147 mg; 29 early-stage corpora lu- tea.

Estimated Age of the Raccoon in Months ^a	Weight in Kilograms	Injection Date ^b	Dose (each) ^c	Hormone	Laparotomy or Autopsy Date and Results
53	5.35	12-2-59-12-13-59 12-14-59	50 IU 200 IU ^j	PMS PMS	12-1-59: Ovaries 10 x 16 mm.
					12-14-59: Ovaries 12 x 6 mm; 9 follicles 2 mm diam in each ovary.
					12-16-59: Left ovary 12 x 6 mm; follicles 2 mm, ready to ovulate.
					12-17-59: Blood oozed from follicles. Left ovary 242 mg, 10 x 6 mm; 6 early-stage corpora lutea 2,000 microns diam.
14	4.54	6-25-57-6-29-57 6-30-57	Unsuccessful Attempts 100 IU 500 IU	PMS PMS	12-19-59: Right ovary, 8 ear- ly-stage corpora lutea 2,400 mi- crons diam; 3-4 corpora lutea with ova.
					7-1-57: Right ovary, 3 follicles 1,075 x 1,400 microns; no cor- pora lutea.
					8-13-57: Left ovary, follicles to 480 microns; no corpora lu- tea.
					9-4-59: Large follicles, none ovulated.
4	4.44	8-24-59-9-2-59 9-3-59 9-4-59	12.5 mg 50 IU ^m 1,000 IU ^j 2,000 IU ^j	P ⁱ PMS CGH ^a CGH	9-7-59: Ovaries 1,277 and 1,784 mg; 20 follicles, 2,544 x 3,265 microns, in each ovary; no ovulations.

Table 12.—Continued

Estimated Age of the Raccoon in Months ^a	Weight in Kilograms	Injection Date ^b	Dose (each) ^c	Hormone	Laparotomy or Autopsy Date and Results
28	4.40	8-24-59—8-30-59	100 IU	PMS	8-31-59: Died; follicles to 1,030 microns.
5	4.35	9-30-59—10-4-59	100 IU	PMS	10-5-59: Died; ovaries 252 mg; follicles to 160 microns. 4-2-58: Left ovary removed; 4 corpora lutea.
12	4.94	6-18-58—6-22-58	10 AU	FSH	6-23-58: Right ovary, 25 or more follicles to 875 microns.
2	1.50	7-16-58—7-20-58 7-21-58	10 AU; 500 AU ^d	FSH LH	7-24-58: Right ovary removed; packed with follicles to 140 microns.
39	3.95	9-8-58—9-12-58 9-15-58—9-23-58 9-22-58—9-23-58	15.6 mg 5 AU 50 AU ^d	P FSH, LH LH	9-24-58: Left ovary, follicles to 219 microns.
19	5.72	7-16-58—7-20-58 7-21-58	20 AU 50 AU ^d	FSH LH	7-24-58: Ovaries removed; 17-20 follicles to 875 microns; ova in follicles.
		12-4-58—12-8-58	10 AU 5 AU	FSH LH	12-10-58: Ovaries 7 x 5 mm.
		12-9-58	200 IU ^d	PMS	
		12-10-58—12-14-58	10 AU 5 AU	FSH, LH	
		12-16-58	200 IU ^d	PMS	
		12-17-58	15 AU 10 AU	FSH LH	12-17-58: Ovaries 10 x 7 mm; small follicles.

Estimated Age of the Raccoon in Months ^a	Injection Date ^b	Dose (each) ^c	Hormone	Laparotomy or Autopsy Date and Results
19 (cont.)	12-18-58-12-21-58 12-22-58	10 AU 100 IU ⁱ	FSH, LH LH	12-23-58: Left ovary removed, 282 mg, 11 x 6 mm; 25 follicles to 1,115 microns. 5-5-59: Right ovary 11 x 7 mm.
23	5-7-59-5-11-59 5-13-59	10 AU 200 AU ⁱ	FSH, LH LH	5-14-59: Right ovary removed; 3 old corpora lutea. 4-2-58: Right ovary removed; 3 corpora lutea.
14	9-15-58-9-19-58 9-22-58-9-23-58	10 AU 50 AU ⁱ	FSH, LH LH	9-25-58: Left ovary 1,180 mg; many follicles 850 x 2,545 mi- crons; ova in 3.
17	6-22-59-6-23-59 6-25-59-6-26-59 6-28-59 6-30-59 7-2-59	10 AU 10 AU 200 AU ⁱ 500 U 500 U ⁱ	FSH, LH FSH, LH LH CGH CGH	6-30-59: Ovaries 12 x 6 mm; 12 follicles in each. 7-2-59: Ovaries 17 x 7 mm; follicles twice as large as on 6- 30-59. 7-6-59: Left ovary removed; follicles 1,475 microns. 7-13-59: Right ovary removed; several luteinized follicles 825 microns and smaller.
17	8-24-59-9-5-59 9-7-59	10 AU 200 AU ⁱ	FSH, LH FSH, LH	9-7-59: Ovaries 11 x 7 mm. 9-8-59: Ovaries removed; 11- 15 follicles 1,150 x 1,300 mi- crons in each.

Table 12.—Continued

Estimated Age of the Raccoon in Months ^a	Weight in Kilograms	Injection Date ^b	Dose (each) ^c	Hormone	Laparotomy or Autopsy Date and Results
2	1.04	7-7-59—7-13-59 7-14-59 7-16-59 7-17-59 ^d	2 AU 10 AU 150 U 200 U ^e	FSH, LH FSH, LH CGH CGH	7-20-59: Ovaries 7 x 5 mm, total weight of both ovaries 104 mg; a few follicles to 100 mi- crons.
4	1.54	7-22-59—7-29-59 7-30-59 7-31-59	50 IU 100 IU 250 IU	PMS PMS PMS	8-3-59: Right ovary removed, 9 x 4 mm, 28 mg; follicles to 105 microns.
3	2.13	7-22-59—7-30-59 7-31-59	10 AU 25 AU	LH LH	8-3-59: Right ovary removed, 7 x 4 mm, 39 mg; follicles to 200 microns.
2	0.91	7-22-59—7-23-59 7-24-59—7-30-59	408 mg 425 mg ^m	HMG-J5 ^o HMG-J5	8-3-59: Right ovary 7 x 3 mm, 34 mg; few follicles to 109 mi- crons.

^a Estimated age as of the first injection date shown in the table.^b One injection was given on each date listed except as otherwise noted.^c All injections were subcutaneous unless otherwise noted.^d The injection was intramuscular.^e Pregnant mare's serum.^f AU = Armour Units.^g Follicle-stimulating hormone.^h Luteinizing hormone.ⁱ FSH, LH indicates that the hormones were mixed and injected; equal quantities of each were given except as noted.^j The injection was intravenous or via cardiac puncture.^k The injection was intraperitoneal.^l Progesterone.^m Two injections were given daily.ⁿ Chorionic gonadotropin hormone.^o Human menopausal gonadotropin.

cutaneous injections of PMS at the rate of 100 IU daily for 12 days were begun in September. Many large follicles were found on the 13th day of treatment. This female was given 550 IU of PMS intravenously on the 13th day. Seventy-two hours later many *blut punkte* were observed in each ovary. The left ovary (826 mg) and a piece of the uterus were removed. Histological examination revealed 26 corpora lutea in early stages. Most had blood in the lumina and appeared to be freshly ovulated. The uterus showed a fairly typical effect of estrogen, and no material was present in the uterine glands, indicating the near absence of progesterone. Eleven days later (26 days after the first injection) the female was killed and the right ovary was removed (2,147 mg). There were 29 early-stage corpora lutea, most of them packed with luteal cells, but lumina were present in 2-4 corpora. The cytoplasm and nuclei of these luteal cells were more darkly stained and the nuclei were smaller than usual. The intracellular space exceeded the norm. Secretory material was present in the uterine glands.

The third female was about 22 months old when caught, but was 53 months of age when these experiments were begun. Subcutaneous injections of PMS were begun 2 months before the breeding season, at the rate of 50 IU per day, and were continued for a total of 12 injections. On the 13th day 200 IU were injected intravenously. At that time each ovary measured 12 X 6 mm and contained approximately nine follicles, each about 2 mm in diameter. Two days later the ovaries and follicles had not changed in size, but one follicle was hemorrhagic and one had a thin red line across the surface at its highest point. Twenty-four hours later when the ovaries were examined, blood oozed from most or all of 11 or 12 follicles in each. There were tiny holes in the highest points of most, and perhaps in all, of them. The ovulated follicles were partly hollow and partly filled with fluid and stringy material. The left ovary, measuring 10 X 6

mm, was removed (242 mg). When examined histologically, it was found to contain six or more blood-filled, early-stage corpora lutea. Among 16 wild raccoons the average number of corpora lutea per ovary, determined by histological examination, was 2.1. Thus, in this most nearly normal ovulation induced by exogenous hormones, the ovaries were somewhat less than twice normal weight, but the ovulation rate was approximately 5.7 times normal.

The female just discussed weighed 5.35 kg and received a total of 800 IU of PMS, a dosage of about 150 IU per kg, a rate similar to that used successfully to cause ovulation in ranch mink (Hammond 1952:219).

In a third series of experiments four different hormones were used on four sexually immature female raccoons from 2 to 4 months old (the last four animals in Table 12) in an attempt to learn how immature ovaries respond to hormones and to study differential responses to the several hormones. The injection of human menopausal gonadotropin (HMG-J5, largely FSH) subcutaneously twice a day for 7 days immediately after 2 days of single injections resulted in little stimulation of either the ovary or the uterus in one immature female. In the second young raccoon 50 international units (IU) of PMS daily for 8 days, followed by 100 IU and 250 IU on the 9th and 10th days, respectively, resulted in a slightly more stimulated uterus than did the HMG-J5 injected into the animal just discussed. In the third animal in this age group 10 Armour units of LH injected subcutaneously daily for 9 days, followed by 25 units on the 10th day, resulted in larger follicles than did either of the two previous treatments.

In the raccoon that received only LH this hormone caused more development of the follicles than did either PMS or HMG-J5 in the other young females. PMS and HMG-J5 contain both FSH and LH and might be expected to cause greater stimulation than LH alone. The ovaries stimulated by HMG-J5 contained

more interstitial tissue than did the ovaries of the females that received the other hormones, and the ovaries of the raccoon that received PMS had less interstitial tissue than those of the female that received LH. The uterus of the female injected with HMG-J5 was somewhat less stimulated (endometrium 650 microns) than that (endometrium 820 microns) of the female that was given PMS although the differences in these uteri were slight. The uterus of the female that received LH was more stimulated (endometrium 1,275 microns) than was either of the other two.

On the basis of the information obtained from our experiments with four female raccoons, it appears that 35-50 IU of PMS given subcutaneously each day for 12 days caused the development of follicles at any time of year in adult females. A dose of 200 IU given on the 13th day might be expected to cause ovulation 48-60 hours later.

UTERINE MILK

Uteri, and ovaries containing corpora lutea, were sectioned from 18 raccoons that had not been treated with hormones. In 17 of the 18 secretory material (uterine *milk*) was present in the lumina of most, but not all, of the uterine glands although it may have been present in all 18 uteri but overlooked in some of the sections.

Histological sections of ovaries containing no corpora lutea and the corresponding uteri were examined from 89 raccoons collected throughout the year. February and March were each represented by a single animal, but each other month was represented by three or more animals. The uterine sections from these animals, with two exceptions, contained no secretory material in the endometrial glands. Small amounts of secretory material were present in the uterine glands of one nulliparous adult killed in September and in another, approximately 7 months of age, collected in November. Secretory material was not abundant in either one, but was definitely present.

These data indicate that, in the raccoon, secretory material (presumably uterine milk) is present when corpora lutea are present. In one female, judged to have been only 10 days prepartum, secretory material was present.

Progesterone alone or in combination with estrogen was probably responsible for the secretion of uterine milk (Table 13). Progesterone alone was given for an insufficient length of time to determine whether it alone can cause the uterine glands to secrete. Two castrated females (No. 1297 and 1786) received a combination of progesterone and estrogen for several days, and the endometrial glands of both contained uterine milk (Table 13). Any combination of gonadotrophic hormones that resulted in the formation of corpora lutea caused secretion by the uterine glands. Five treatments of 2.5 mg each of estradiol over periods of 10 and 20 days, respectively, did not cause secretion by the uterine glands in one castrated female. One intact female (No. 2184B) received five daily injections of 20 units each of FSH, followed on the 6th day by 50 units of LH. Three days later, when she was killed, each ovary contained approximately 20-30 follicles measuring up to 750 X 1,250 microns, but no corpora lutea. The lumina of a few endometrial glands contained small bits of secretory material. Several hormones, including various combinations of FSH, LH, CGH, PMS, and HMG-J5, were given to intact females. Except possibly in the female just discussed, none of these hormones caused the uterine glands to secrete except indirectly by causing the formation of corpora lutea.

Methods described by Pearse (1960: 265-271) and by Lillie (1954:274-299) were used in an attempt to demonstrate the nature of the secretory material. In no case did digestion with either ptyalin or diastase remove the secretory material from the endometrial glands. This finding was taken as evidence that it was not glycogen. According to the information on the identification of carbohydrate-containing materials given by

Table 13.—Presence of secretory material in the uterine glands of captive raccoons as related to injections of exogenous hormones.

Raccoon Number	Estimated Age in Months	Hormone	Number of Days After First Treatment	Corpora Lutea	Uterine Milk
1292	24	PMS ^a	28	+ ^b	+
1297	14	PMS	49	—	—
	22	Progesterone, estrogen	70	Castrated	+
1298	53	PMS	15	+ ^c	—
			27	+	+
1782	14	Estradiol	10	Castrated	—
		Estradiol	20	Castrated	—
1786	24	Progesterone, estradiol	28	Castrated	+
2184B	38	FSH ^d , LH ^e	8	—	T ^f
2276	14	FSH, LH, CGH ^g	14	—	T
			21	+	T
2525	19	FSH, LH, PMS	19	—	—
2805	3	LH	12	—	—

^a Pregnant mare's serum.^b The plus symbol indicates the presence of corpora lutea or uterine milk, and the minus symbol indicates their absence.^c Early stage.^d Follicle-stimulating hormone.^e Luteinizing hormone.^f T=traces.^g Chorionic gonadotropin hormone.

Pearse (1960:236-237), it was either a mucoprotein or a glycoprotein.

SUMMARY

1.—The testes of raccoons in Illinois grew at a uniform rate from birth until about 10 months of age; at that time the average weight of one testis was 5.6 grams. Most male raccoons reached sexual maturity as yearlings, but juvenile males became sexually potent 3-4 months later in the year than did adult males. Seasonal variations occurred in testis weights; the average weights were minimal in June, July, and August, and were highest in December. The average maximum weight of one testis was 2.8 times the average minimum. There was a positive correlation between testis weight and the presence of sperm in the epididymis, but the weight of the testis did not infallibly indicate whether sperm was present in the epididymis. In a large group of raccoons sperm may be found in some animals at any given time, but individual males had periods averaging

3-4 months when they were incapable of breeding.

2.—Ovaries of raccoons showed a nearly steady rate of growth from birth in April through the following November. The heaviest normal ovaries found were in juveniles during November, approximately 3 months prior to the peak of the breeding season. The ovaries of juveniles declined in weight from November through January, and perhaps through March. Seasonal weights of ovaries in parous raccoons followed a pattern similar to that found in the gonads of adult males. The minimum average weight was reached in July, with a slow but consistent increase in weight occurring from then until November. The weights of ovaries of parous raccoons declined from November to December but increased during January and reached their peak average in April, when they were slightly heavier than they were in November. The average peak weight of ovaries of adults in April was slightly more than 1.6 times their average weight in July.

3.—The mean birth date for 20 litters

conceived in the wild was April 18 (range, March 9–June 24) and for 11 litters conceived and born in captivity it was April 24 (range, March 16–June 3).

4.—The measurement of the largest external uterine swelling enabled us to estimate birth dates with a maximum error of 4 days.

5.—The sex ratios of young raccoons less than 2 months of age and of embryos and young at birth were not significantly different from 50:50, but there were more males among the young less than 2 months old than among the other group, possibly indicating some differential mortality of females between birth and 2 months of age.

6.—Yearling females either bred when adults bred or did not breed until they were almost 2 years of age. If female raccoons ovulated but did not become pregnant, if they aborted or resorbed their young, or if they lost their young at or near birth, they sometimes ovulated a second time in one season. The interval between ovulations in five captive raccoons held in Urbana, Ill., varied approximately from 80 to 140 days. Severe weather conditions (extreme cold or deep snow) interfered with the normal breeding cycle and resulted in an unusually large number of late litters. Female raccoons sometimes gave birth to two litters in one season, but they did not rear more than one litter in one season. The vaginal smear was no more specific for indicating estrus than was gross vulval swelling.

7.—Contrary to published reports, the raccoon is a spontaneous ovulator. Ovulation was followed by the formation of corpora lutea whether the animal became pregnant or pseudopregnant. The formation of corpora lutea always resulted in changes in the uteri and nipples. The nipples always enlarged; some became heavily pigmented, some became slightly pigmented, and others remained unpigmented. Thus, it was possible to determine whether a female raccoon had ovulated by examining her nipples. Corpora lutea in both isolated and non-isolated pseudopregnant females formed

from ovulated Graafian follicles and not from luteinization of follicles. Corpora lutea persisted in pregnant females until parturition and apparently disappeared 14–16 days after parturition.

8.—Raccoons that ovulate become either pregnant or pseudopregnant, and the corpora lutea persist for about the same time in pseudopregnant raccoons as they do in those that give birth to young. Corpora in females that went at least halfway to term persisted about the same length of time whether the young were aborted, were resorbed, or were born and were removed at birth or nursed until weaned. Field evidence indicated that in Illinois about 2.5 percent of the adult females were pseudopregnant each year.

9.—Ten of 21 captive yearling females and 9 of 14 wild yearling females were sexually immature.

10.—Interstitial tissue occurred in the ovaries at some stage of the reproductive cycle, often occupying as much as 50–90 percent of the space in the ovary, but seldom occurred when corpora lutea were present. Ovaries of females less than 2 months old did not contain large amounts of interstitial tissue, but with this exception the ovaries of females less than 12 months of age contained, on the average, more interstitial tissue—both relatively and absolutely—than did those of older females. From January through June, ovaries of adults contained little interstitial tissue even when corpora lutea were not present; from July through December, ovaries from adults contained more interstitial tissue than did those collected earlier in the year. The greatest abundance of interstitial tissue was in ovaries taken from juveniles during October and November, and the maximum ovarian weights recorded during this study were those of juvenile females in November.

11.—The placenta of *Procyon* is deciduous, as in the dog, cat, fox, and seal, and is endotheliochorial. If used with caution, placental scars in raccoons are useful for estimating litter size and rate of productivity. The significance of multiple groups of scars is not clear, but

it appears that each embryo that reaches 1 month of age is represented by one scar that persists for 10 or more months. Scars in wild females with only one group of scars probably reflect implantation rates for the preceding breeding season. Placental scars apparently persist longer in wild females than in captives.

12.—The reproductive system of the male raccoon is similar to that of the dog; seminal vesicles and Cowper's glands are lacking.

13.—The uterus of the raccoon is intermediate between the bicornuate and the bipartite uterus. There is a single cervix and the horns are distinct, but after they join externally to form the single uterine body, the uterine lumina remain separate to a point near the cervix. The ovoid ovary is completely surrounded by the bursa ovarii. The sac is intact except for a small slit on one side, not large enough to permit passage of the ovary, as in the mink, dog, and fox.

14.—The level of sex hormones in the male affected the enlargement of the preputial orifice and the maturation of

the penis bone but had little or no effect prior to 7 months of age. Castration in the male also apparently caused a slight delay in the closure of the epiphyseal cartilage in the radius and ulna. Removal of the ovaries, even after raccoons had reached sexual maturity but before the epiphyses had closed, delayed the rate of epiphyseal closure.

15.—Embryos persisted for about 19 days after castration in each of two raccoons—to 33 days short of term in one female and 7 days short of term in the other.

16.—Limited studies indicated that injections of androgen did not initiate nor prolong spermatogenesis and apparently did not influence the size of the testes.

17.—A dose of 35–50 IU of pregnant mare's serum given subcutaneously each day for 12 days caused development of Graafian follicles in adult females at any time of the year. A dose of 200 IU given on the 13th day caused ovulation 48–60 hours later; however, in all cases of successful ovulation, the ovaries were much larger—and the rates of ovulation much higher—than normal.

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BULLETIN

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ILLINOIS
Natural History Survey
BULLETIN

**Nutritional Responses
of Pheasants to Corn,
with Special Reference
to High-Lysine Corn**

Ronald F. Labisky
William L. Anderson

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Frontispiece.—Body condition of juvenile hen pheasants fed exclusive diets of normal corn, commercial flight and maintenance chow (FMC), or high-lysine corn for a period of 8 weeks in late autumn. The changes in body weight of these hens, which typified their respective dietary groups at the completion of the feeding trial, were —9 g for normal corn, and +101 g and +41 g for FMC and high-lysine corn, respectively.

Nutritional Responses of Pheasants to Corn, with Special Reference to High-Lysine Corn

Ronald F. Labisky
William L. Anderson

IN LATE 1963, Purdue University scientists discovered, by amino acid analysis, that the endosperm of maize (*Zea mays*) kernels homozygous for the *opaque-2* mutant contained about 70 percent more lysine than the endosperms of kernels of normal hybrids (Mertz et al. 1964; Mertz 1966:12). The endosperm of *opaque-2* also contained greater amounts of tryptophan than that of normal corn (Pickett 1966:19).

Lysine and tryptophan are among those amino acids that are dietary essentials for protein synthesis in many animals, including man. The proteins in endosperm of normal corn are of low biological quality. Thus the *opaque-2* mutant, which alters the amino acid composition (particularly that of lysine, tryptophan, and leucine) of the maize endosperm, has offered the potential of a type of corn having exceptional nutritional values. The superior nutritional benefits of this modified-protein corn (hereinafter termed *high-lysine corn*) for growth have already been demonstrated in feeding experiments with rats (Mertz et al. 1965; Mertz 1966), swine (Pickett 1966; Jensen et al. 1967), chicks (Rogler 1966), and turkeys (Adams & Rogler 1970).

The nutritional potential of high-lysine corn has led to predictions that this corn may replace a substantial acreage of normal-corn hybrids produced in the Corn Belt during the 1970's. The estimated acreage of high-lysine corn planted in the United States in 1972 was 80,000–100,000 acres (D. E. Alexander, University of Illinois, personal communication, January 12, 1973). Inasmuch as corn is important in the diet of many wild animals, the widespread use of high-

lysine corn offers a potential nutritional benefit to wild birds and mammals.

Corn figures more prominently in the diet of midwestern pheasants, particularly in fall and winter, than it does for most wildlife species (Korschgen 1964: 170, 173). To illustrate, during fall and winter, corn constitutes at least 80 percent (by weight) of the total food intake by pheasants in thriving populations in east-central Illinois (Anderson & Stewart 1969:261; R. F. Labisky, unpublished data). Yet despite the importance of corn to pheasants, little is known of its nutritional attributes for growth, maintenance, or reproduction. Furthermore, juvenile hens, in contrast to adult hens, suffer a disproportionately high rate of nonhunting mortality between fall and winter in Illinois (R. F. Labisky, unpublished data). That the onset of this mortality among juvenile hens coincides with that time of the year at which waste corn from the harvest suddenly becomes abundantly available suggests a potential causal link between unbalanced nutrition and mortality. Hence the objectives of this study were to ascertain the physiological responses of juvenile hen pheasants in fall, and of adult hen pheasants in late winter and early spring, to exclusive diets of both normal corn and high-lysine corn.

ACKNOWLEDGMENTS

Acknowledgment is due the following members of the Department of Agronomy, University of Illinois. Dr. D. E. Alexander supplied the corns, provided their lysine and fatty acid profiles, and offered advice on various aspects of the

study. Dr. T. R. Peck and G. G. Stone offered laboratory facilities for, and materially aided in, the analyses of pheasant excreta for nitrogen. Dr. I. de la Roche analyzed the fat samples for determination of fatty acids. Dr. C. M. Wilson analyzed the commercial ration for amino acids.

Dr. B. G. Harmon, Department of Animal Science, University of Illinois, supervised the analyses of pheasant excreta for lysine.

Dr. G. C. Sanderson, Illinois Natural History Survey, offered editorial suggestions during preparation of the paper, and O. F. Glissendorf edited the final manuscript. D. R. Vance and J. E. McClendon of the Survey assisted in various aspects of the experiment.

Special thanks are due Drs. Alexander and Harmon, and Dr. J. E. Savage, Department of Poultry Science, University of Missouri, for critically reviewing the manuscript.

METHODS

FEEDING TRIAL I: JUVENILE HENS

The 21 juvenile hens used in the experiment were obtained from the Illinois State Game Farm, Yorkville, in 1966. These hens, which had hatched on June 20, were transported to Urbana on September 13. The hens were held in two wire-bottomed 3.0 x 3.9 x 1.8-meter pens and fed a commercial flight and maintenance chow (FMC) until October 3 when they were individually placed, by random assortment, in 70 x 60 x 34-cm cages. The cages had thin-walled fiberglass sides, top, bottom, and rear, which prevented sight contact between birds. The birds were fed a diet of two-thirds FMC and one-third normal corn (whole kernels) for the period October 3-14 to acquaint them with corn, and then an exclusive diet of FMC for the period October 15-20.

Inasmuch as 19 of the 21 hens posted gains in body weight between Octo-

ber 10 and October 20, the feeding trial was begun on the latter date. Three groups of 7 hens each were randomly selected to be fed exclusive, unrestricted diets of FMC, normal hybrid corn (Pioneer 3306), or high-lysine corn (Table 1), and water ad libitum. The FMC was pressed into corn-sized pellets for the feeding trials (see Frontispiece). The experiment was terminated 8 weeks later, December 15. One hen from the group of hens fed normal corn died from an injury during the trial.

FEEDING TRIAL II: ADULT HENS

The 12 adult hens, 3 and 4 years old, used in the feeding trial were also of game-farm origin. These hens had been transported to Urbana as juveniles, and subsequently maintained in wire-bottomed outdoor pens, similar to those used to house the juveniles. On February 7, 1967, these hens were individually placed, by random assortment, in the same cages in which the juveniles of Trial I had been held. They had been fed an introductory diet of one-half FMC, one-fourth normal corn, and one-fourth high-lysine corn for the period February 1-7. Because of their quick acceptance of corn, they were returned to an exclusive FMC diet on February 8.

All 12 hens posted gains in body weight during the interval of February 27-March 6; therefore, the feeding trial was begun on the latter date. Six hens were offered a diet of normal corn and six hens a diet of high-lysine corn (Table 1); both groups had unrestricted access to water. The food intake by adult hens was restricted to 200 g of corn per bird per week. The corn was provided in two 100-g lots, on the first and fourth days of each week. This limited offering of corn was judged to be about 60 percent of a normal weekly intake, and was intended to simulate the estimated potential food intake of wild hens subjected to the rigors of late winter in Illinois. The experiment was terminated after 7 weeks, on April 24.

Table 1.—Mean concentrations of calories, crude protein, lysine in protein, and selected minerals in diets of a commercial flight and maintenance chow (FMC), of normal corn, and of high-lysine corn that were fed to hen pheasants in 1966 and 1967.

	Diets		
	FMC	Normal Corn: Pioneer 3306	High-Lysine Corn: <i>Opaque-2</i> Synthetic A.
Calories per g ^a	4,278.9 ± 4.4 ^b	4,651.6 ± 99.1	4,544.0 ± 6.1
Percentage crude protein ^c	22.8 ± 0.03	12.0 ± 0.1 ^d	11.7 ± 0.1
Percentage lysine ^c in protein	4.9	3.2 ^d	4.7
Percentage fiber	≤12.0	2.0	2.0
Percentage saturated: unsaturated fatty acids ^f	^g	14:86	19:81
ppm of major elements			
calcium	14,443 ± 1,469	41 ± 3	38 ± 1
magnesium	1,833 ± 24	1,166 ± 48	972 ± 37
sodium	2,785 ± 49	204 ± 9	195 ± 4
potassium	7,997 ± 159	3,249 ± 138	3,924 ± 184
phosphorus	5,327 ± 220	2,183 ± 250	2,264 ± 202

^a Caloric contents of the rations differed significantly ($F=11.18_{2,6}$; $P<0.05$); application of Duncan's multiple range test indicated that the caloric content of both corns differed from FMC but not from each other.

^b Standard errors.

^c Crude protein compositions of the rations differed significantly ($F=989.66_{2,12}$; $P<0.05$); application of Duncan's multiple range test indicated that the caloric content of both corns differed from FMC, but not from each other.

^d This particular hybrid contains slightly greater concentrations of protein and of lysine than most normal corn hybrids. The average normal corn hybrid contains about 10.5 percent protein, of which 2.8 percent is lysine.

^e Lysine content is for defatted samples.

^f The principal fatty acids in the corns are unsaturated: oleic and linoleic. The normal and high-lysine corns contained, respectively, 34 and 22 percent oleic, and 52 and 58 percent linoleic acid.

^g Data are not available.

COLLECTION OF DATA

Body weights of the hens were recorded at the onset of the feeding trials and at weekly intervals thereafter. Correspondingly, the amount of food consumed by each hen during each week of the feeding trial was measured to the nearest gram. All food consumption was converted to a dry weight standard. The total excreta was collected for each juvenile hen for Weeks 4, 5, 6, 7, and 8 (final) and for each adult hen for Weeks 5 and 7 (final).

After the final body weight of the hens had been recorded, each hen was placed in an inverted position and decapitated. All birds were then dissected. The following muscles, fat deposits, organs, and glands were excised from both juvenile and adult hens, and weighed: muscles of right half of the sternum (*pectoralis thor-*

acia, ventral head of the *supracoracoideus*, and *coracobrachialis*—nomenclature as used by Hudson & Lanzillotti 1964: 13–15); fat strip and visceral fat (as described by Breitenbach & Meyer 1959: 1017); liver; thyroids; parathyroids; and adrenals. The heart, pancreas, gizzard, kidneys, spleen, and thymuses from juvenile hens were also excised and weighed, as were the ovary, oviduct, and largest ovum from the adult hens. The organs and glands, after being freed of extraneous material, were blotted carefully with paper toweling to remove excess blood and moisture prior to being weighed. The heart and liver were opened and blood clots therein removed; the gall bladder was excised from the liver. The contents, but not the lining, were removed from the gizzard before the latter was weighed. The weights

recorded for kidneys and endocrine glands are for paired (right and left) measurements.

ANALYSES

Each sample of food and excreta was oven-dried at 60°C for 142 hours, finely ground, and then sealed in a sterile plastic bag for subsequent determination of nitrogen (crude protein), lysine, and caloric content.

Nitrogen content of foods and excreta was determined by Kjeldahl procedures; the crude protein content of each item was calculated as nitrogen $\times$ 6.25. Crude protein determinations were made for five samples of each of the three foods, and for single samples of dried excreta from each juvenile hen for each of the last 5 weeks of the 8-week experiment and for each adult hen for Weeks 5 and 7 of the 7-week experiment.

Lysine in the pheasant excreta was measured, following acid hydrolysis under vacuum for 16 hours, by chromatographic analysis (Beckman Amino Acid Analyzer, Model 120). Lysine determinations for excreta were made from composites of the weekly samples for Weeks 4–8 of the 8-week experiment for each juvenile hen, and for Weeks 5 and 7 of the 7-week experiment for each adult hen. The amount of lysine in the foods (defatted) was also measured by chromatographic analysis; approximately 80 percent of the nitrogen in the foods was recovered as amino acids.

Caloric content of foods and excreta was measured by standard caloric-bomb techniques. Calories were measured from three samples of each of the three foods, and from a composite of the five and two weekly collections of excreta from each juvenile and each adult hen pheasant, respectively.

The mineral content of the foods was derived by atomic absorption spectrophotometry (for Ca and Mg), flame spectrophotometry (for Na and K), and colorimetry (for P).

The null hypothesis, in all tests for determination of statistical differences, was accepted or rejected at the 0.05 level of probability.

FINDINGS

JUVENILE HENS

Body Weight Changes

The juvenile hens that were fed exclusive diets of FMC or high-lysine corn posted gains in body weight that averaged 98.4 and 23.4 g, respectively, during the 8-week feeding trial; those fed normal corn suffered losses that averaged 8.7 g (Table 2). Both groups of hens to which corn was fed exhibited marked declines in body weight during the first week of the feeding trial (Fig. 1). In the final analysis, all of the seven hens fed FMC, five of the seven hens fed high-lysine corn, and three of the six hens fed normal corn gained weight during the

Table 2.—Body weight statistics for juvenile hen pheasants fed exclusive diets of flight and maintenance chow (FMC), of normal corn, or of high-lysine corn for an 8-week period, October 20–December 15, 1966.

	Mean Body Weight (g) or Weight Change for Specified Diet			F Values _(df)
	FMC (n=7 Hens)	Normal Corn (n=6 Hens)	High-Lysine Corn (n=7 Hens)	
Initial weight (October 20)	711.3 $\pm$ 29.2*	742.2 $\pm$ 36.9	752.7 $\pm$ 32.4	0.45 _{2,17}
Final weight (December 15)	809.7 $\pm$ 29.6	733.5 $\pm$ 35.8	776.1 $\pm$ 39.6	1.13 _{2,17}
Weight change	+98.4 $\pm$ 7.6	–8.7 $\pm$ 14.7	+23.4 $\pm$ 27.8	4.70 _{2,17} *

* Denotes statistical significance, $P < 0.05$. All combinations of paired means differed significantly.

* Standard errors.

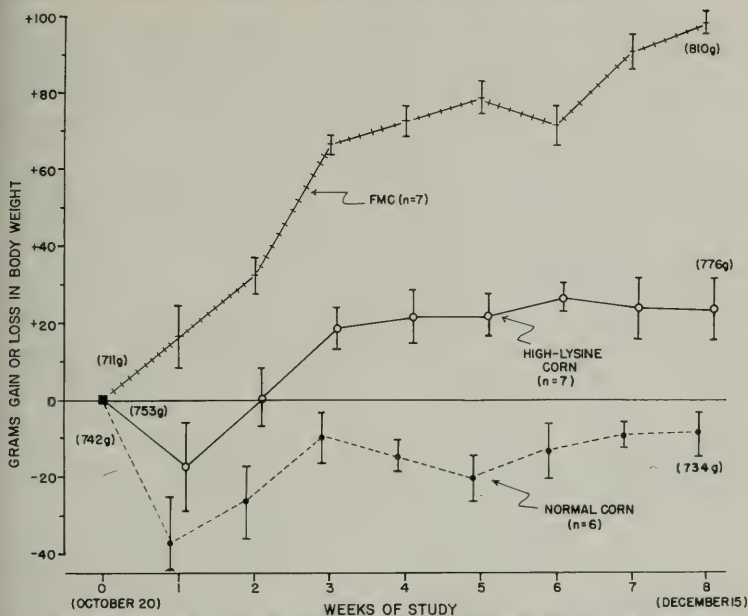


Fig. 1.—Mean change in body weight (g) by weekly periods among juvenile hen pheasants fed exclusive diets of FMC, of normal corn, or of lysine corn; the vertical lines transecting the means are standard errors. The mean initial and final body weights for each group are given at the left and right of the graph, respectively. Statistically significant ($P < 0.05$; 2 and 19 df) weight changes occurred among diets for three of the eight successive weekly periods: initial to 1 ($F = 3.73$); 2 to 3 ($F = 3.93$); and 6 to 7 ($F = 3.59$).

8 weeks. The extremes in weight change among hens on each of the diets were: FMC, +128 and +59 g; high-lysine corn, +177 and -88 g; and normal corn, +44 and -71 g.

Food Consumption

The three diets, fed ad libitum, were consumed by the juvenile hens in significantly different amounts; the greatest intake was of FMC and the lowest was of normal corn (Table 3). Inasmuch as the caloric, crude protein, and lysine contents of the high-lysine corn were either similar to or greater than those of normal corn (Table 1), thereby discounting compensatory nutritional needs, the greater rate of consumption of high-lysine corn

per hen suggested that it may have been more palatable¹ to pheasants than normal corn. Changes in body weight per 100 g of food consumed averaged +4.3, +1.3, and -0.5 g on FMC, high-lysine corn, and normal corn, respectively.

Digestibility Coefficients

Significant differences in the digestibility coefficients² were exhibited by hens

¹ Food intake is often depressed if the animal's diet is deficient in either protein or an indispensable amino acid (see review by Harper, 1967). Therefore, the greater consumption of high-lysine corn over normal corn by the hens may have reflected its higher lysine content rather than any superiority in palatability.

² Digestibility coefficient =

$$[1 - \left(\frac{\text{Total dry weight of excreta}}{\text{Total dry weight of food consumed}} \right) \times 100]$$

on the different diets (Table 3). Hens fed FMC digested substantially less (59.1 percent) of their ration than did those hens fed either normal corn (82.5 percent) or high-lysine corn (81.2 percent). In contrast to the corns, the comparatively low rate of digestibility of FMC, in part, reflected its higher fiber content. Despite the similarity in the mean digestibility coefficients of the two corns, they were significantly different because of the extremely narrow range of variation in the digestibility of each of the corns by the individual hens.

Calorie Utilization

Although the total intake of calories by the juvenile hens was significantly greater for those fed FMC than for those fed either normal corn or high-lysine corn, the utilization of the calories by the hens receiving the FMC was markedly less than for those receiving either of the corns; the metabolizability coeffi-

cients³ were 66.3, 84.8, and 83.3 for FMC, normal corn, and high-lysine corn, respectively (Table 4). Because of this different proportionate utilization of calories, there was no significant difference in the total number of calories utilized per hen for birds on the three diets during the 8-week trial. Juvenile hens obtained 2,837, 3,945, and 3,808 kcal of metabolizable energy per kg of FMC, normal corn, and high-lysine corn consumed, respectively.

Protein Utilization

The intake of crude protein by the juvenile hens was significantly different among the birds fed the three diets, being more than twice as great for FMC as for either normal or high-lysine corn (Table 3). The high intake of crude protein by the hens fed FMC reflected not only

³ Metabolizability coefficient =

$$\left[1 - \left(\frac{\text{Total calories in excreta}}{\text{Total calories in food consumed}} \right) \times 100 \right]$$

Table 3.—Comparative consumption and utilization of three foods—flight and maintenance chow (FMC), normal corn, and high-lysine corn—fed as exclusive diets to different groups of juvenile hen pheasants for an 8-week period, October 20–December 15, 1966. All values are expressed as dry weight.

	Mean Value per Hen per Week for Specified Diet			F Values ^(a)
	FMC (n=7 Hens)	Normal Corn (n=6 Hens)	High-Lysine Corn (n=7 Hens)	
Food consumed (g)	282.4 ± 12.9 ^a	205.6 ± 10.8	234.6 ± 17.0	65.11 _{2,130} *
Crude protein consumed (g) ^b	64.4 ± 1.0	24.7 ± 1.3	27.5 ± 0.7	888.51 _{2,136} *
Lysine consumed (g) ^c	3.2 ± 0.06	0.8 ± 0.01	1.3 ± 0.03	2,305.51 _{2,130} *
Excreta (g) ^d	115.5 ± 2.1	36.0 ± 0.6	44.2 ± 1.0	716.81 _{2,83} *
Digestibility coefficient (percent) ^d	59.1 ± 0.3	82.5 ± 0.2	81.2 ± 0.3	2,266.67 _{2,83} *
Crude protein in excreta (percent) ^d	39.3 ± 1.5	47.9 ± 0.9	47.2 ± 0.7	20.92 _{2,83} *
Crude protein utilized (g) ^d	16.2 ± 1.8	6.5 ± 0.4	5.7 ± 0.4	24.24 _{2,83} *
(percent) ^d	26.0 ± 2.5	27.2 ± 1.6	21.0 ± 1.4	3.11 _{2,83}
Change in body weight (g)	+12.3	-1.1	+2.9	

* Denotes statistical significance, $P < 0.05$. Those means underscored by the same line are not significantly different. Interactions among weeks yielded no significant F values in any category.

^a Standard errors.

^b See Table 1 for protein content of foods.

^c Product of crude protein consumed and amount of lysine in protein.

^d Based on data for Weeks 4 through 8 only.

Table 4.—Comparative consumption and utilization of calories by juvenile hen pheasants fed exclusive diets of a flight and maintenance chow (FMC), of normal corn, or of high-lysine corn for an 8-week period, October 20–December 15, 1966.

	Mean Value per Hen per 8-Week Period for Specified Diet			F Values _(df)
	FMC (n=7 Hens)	Normal Corn (n=6 Hens)	High-Lysine Corn (n=7 hens)	
Calories consumed (kcal)	9,688 ± 244 ^a	7,501 ± 179	8,357 ± 542	6.76 _{2,17} *
Calories per g excreta ^b	3,359 ± 19	3,892 ± 23	3,888 ± 30	156.99 _{2,17} *
Calories utilized (kcal) ^b	6,409 ± 147	6,486 ± 176	6,959 ± 477	0.91 _{2,17}
(percent) ^c	66.3 ± 0.4	84.8 ± 0.3	83.3 ± 0.2	1,005.63 _{2,17} *

* Denotes statistical significance, $P < 0.05$. Those means underscored by the same line are not significantly different.

^a Standard errors.

^b Product of the 8-week consumption of calories and the 5-week (Weeks 4–8) percentage utilization of calories for each hen.

^c Caloric values for Weeks 4–8.

their high rate of consumption of the ration but also the ration's high protein content (22.8 percent). Whereas the proportionate utilization of the crude protein consumed by the hens did not differ significantly among diets (Table 3), those hens fed FMC utilized nearly 2½ times more crude protein than did hens fed either of the corns. Changes in body weight of the juvenile hens were related directly ($r = 0.56$, 18 df; $P < 0.05$) to the amount of crude protein utilized.

Lysine Utilization

The intake of lysine by the juvenile hens also differed significantly among the

three diets; the hens fed FMC consumed about 2½ and 4 times as much as those hens fed lysine corn and normal corn, respectively (Table 5). The proportionate utilization of lysine, however, was greatest for hens fed high-lysine corn (99.2 percent), and differed significantly from that for hens fed either normal corn (88.4 percent) or FMC (85.6 percent). The total amount of lysine utilized per hen during the 8-week feeding trial differed significantly among the diets, averaging 21.6 g on FMC, 10.2 g on high-lysine corn, and 5.6 g on normal corn. The response in body weight of the juvenile hens was strongly dependent ($r =$

Table 5.—Comparative consumption and utilization of lysine by juvenile hen pheasants fed exclusive diets of a flight and maintenance chow (FMC), of normal corn, or of high-lysine corn for an 8-week period, October 20–December 15, 1966.

	Mean Value per Hen per 8-Week Period for Specified Diet			F Values _(df)
	FMC (n=7 Hens)	Normal Corn (n=6 Hens)	High-Lysine Corn (n=7 Hens)	
Lysine consumed (g)	25.2 ± 0.6 ^a	6.3 ± 0.2	10.3 ± 0.7	314.24 _{2,17} *
Lysine utilized (g) ^b	21.6 ± 0.4	5.6 ± 0.1	10.2 ± 0.7	311.67 _{2,17} *
(percent) ^c	85.6 ± 1.5	88.4 ± 1.0	99.2 ± 0.1	51.24 _{2,17} *

* Denotes statistical significance, $P < 0.05$. Those means underscored by the same line are not significantly different.

^a Standard errors.

^b Product of the 8-week consumption of lysine and the 5-week (Weeks 4–8) percentage utilization of lysine for each hen.

^c Utilization values for Weeks 4–8.

0.73, 18 df; $P < 0.05$) on the amount of lysine utilized.

Protein vs. Lysine

Significant differences existed in the quantitative utilization of both crude protein and lysine by the juvenile hens on the three diets, which warranted a more definitive examination of the contribution of these two variables to the growth and maturation processes of pheasants. Hence, the influences of the quantitative utilization of crude protein and of lysine, irrespective of diets, on the corresponding gain or loss in body weight of the juvenile hens were measured by multiple regression analysis (Table 6). This analysis revealed, as previously demonstrated, that both the amount of crude protein utilized and the amount of lysine utilized, when considered separately, significantly influenced the body weights of juvenile hens in autumn. After accounting for crude protein, the amount of lysine utilized made a significant contribution to regression; however, the interjection of crude protein after accounting for lysine did not reveal a significant contribution to regression. Thus although the body weight of juvenile hen pheasants was significantly dependent on the utilized amounts of both crude protein and lysine when the two variables were considered singly, it was significantly dependent only on the utilized amount of lysine when

the two variables were considered together (Table 6).

Glands and Organs

The mean weights of gizzards, parathyroid glands, adrenal glands, and kidneys differed significantly among the hens fed diets of FMC, normal corn, or high-lysine corn (Table 7). These differences, except in the case of kidneys, also were evident when the weights of the glands or organs were expressed as percentages of body weight.

The size of the adrenal glands, when expressed as an index percentage of body weight, was inversely correlated with the gain (or loss) in body weight of the juvenile hens (Fig. 2), and thus adrenal size was generally greatest for hens fed normal corn, intermediate for those fed high-lysine corn, and least for those fed FMC.

Fat and Fatty Acids

Although the deposits of fat, whether strip or visceral, did not differ statistically among the juvenile hens fed the three diets, they were greatest for juvenile hens fed high-lysine corn, intermediate for those fed FMC, and least for those fed normal corn (Table 7). The accumulations of fat by hens fed high-lysine corn averaged nearly three times greater than accumulations of fat by hens fed normal corn.

The distribution of the fatty acids con-

Table 6.—Analysis of variance, as derived from multiple linear regression analysis, of the effects of the utilized amounts of crude protein (g) and lysine (g) on the gains or losses in body weight (g) of juvenile hen pheasants in autumn. The null hypothesis is that the contribution to regression from X_i is zero, where $i=1$ (crude protein), 2 (lysine).

Source	DF	SS	MS	F
X_1 regression	1	27,974	27,974	10.73*
X_2 regression X_1	1	16,515	16,515	6.33*
Residual	17	44,318	2,607	
Total	19	88,807		
X_2 regression	1	44,392	44,392	17.03*
X_1 regression X_2	1	97	97	0.04
Residual	17	44,318	2,607	
Total	19	88,807		

* Denotes statistical significance, $P < 0.05$.

Table 7.—Mean weights of selected tissues, organs, and glands from juvenile hen pheasants fed exclusive diets of a flight and maintenance chow (FMC), of normal corn, or of high-lysine corn for an 8-week period, October 20–December 15, 1966. Means underscored by the same kind of line are significantly different ($P < 0.05$; 2 and 17 df).

Tissue, Organ, or Gland	FMC (n=7)	Normal Corn (n=6)	High-Lysine Corn (n=7)	Percent of Final Body Weight		
				FMC	Normal Corn	High-Lysine Corn
Sternal muscles	212.0 ± 7.9	189.4 ± 16.8	190.1 ± 8.0	26.2 ± 0.6	25.6 ± 1.0	24.6 ± 0.6
Fat strip	1.03 ± 0.28	0.53 ± 0.12	1.45 ± 0.52	0.12 ± 0.03	0.07 ± 0.02	0.17 ± 0.05
Visceral fat	6.2 ± 1.9	3.1 ± 1.0	10.9 ± 4.3	0.75 ± 0.23	0.39 ± 0.11	1.28 ± 0.44
Liver	12.1 ± 0.7	11.2 ± 1.0	12.6 ± 0.8	1.49 ± 0.06	1.51 ± 0.08	1.63 ± 0.06
Pancreas	1.06 ± 0.05	0.95 ± 0.07	0.94 ± 0.05	0.13 ± 0.01	0.13 ± 0.01	0.12 ± 0.01
Gizzard	<u>10.2 ± 0.3^a</u>	<u>14.6 ± 0.4^a</u>	<u>15.8 ± 0.7^a</u>	<u>1.26 ± 0.03^b</u>	<u>2.02 ± 0.14^b</u>	<u>2.05 ± 0.05^b</u>
Kidneys	4.3 ± 0.1 ^c	3.3 ± 0.2 ^c	3.8 ± 0.1 ^c	0.54 ± 0.02	0.46 ± 0.04	0.50 ± 0.02
Spleen	0.31 ± 0.08	0.27 ± 0.01	0.26 ± 0.04	0.04 ± 0.008	0.04 ± 0.002	0.03 ± 0.004
				Percent (X 10 ¹)		
Thymuses	360 ± 84	259 ± 32	349 ± 83	431 ± 88	364 ± 58	460 ± 111
Thyroids	50.3 ± 7.7	34.9 ± 4.3	38.5 ± 8.2	64.7 ± 12.1	48.7 ± 6.7	51.1 ± 11.9
Parathyroids	<u>4.1 ± 0.9^d</u>	<u>9.9 ± 1.5^d</u>	<u>8.5 ± 0.5^d</u>	<u>5.2 ± 1.2^e</u>	<u>13.7 ± 2.3^e</u>	<u>11.2 ± 0.8^e</u>
Adrenals	<u>55.0 ± 5.6^f</u>	<u>91.2 ± 5.6^f</u>	<u>77.0 ± 7.6^f</u>	<u>68.4 ± 9.8^f</u>	<u>125.7 ± 9.8^f</u>	<u>100.4 ± 6.7^f</u>

^aF = 34.58, ^bF = 31.26, ^cF = 10.35, ^dF = 9.21, ^eF = 8.68, ^fF = 12.66, ^gF = 12.69.

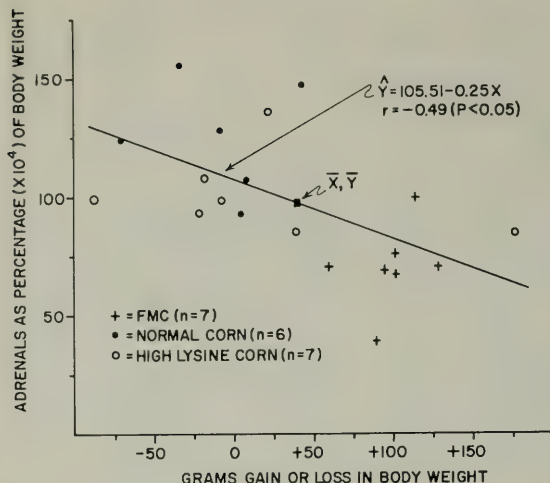


Fig. 2. — Relationship, as indicated by linear correlation, between gain or loss in body weight (g) and the corresponding size of adrenal glands (expressed as 10^4 percentage of final body weight) for juvenile hen pheasants fed exclusive diets of either FMC, normal corn, or high-lysine corn for the total 8-week feeding trial, October 20–December 15, 1966.

tained in the visceral fat of juveniles was almost the same for birds on diets of normal corn and high-lysine corn; the ratio of saturated to unsaturated fatty acids in the visceral fat was about 27:73 for both corn diets (Table 8). The vis-

ceral fat of juvenile hens fed FMC contained a higher proportion of saturated fatty acids than did fat from hens fed either of the two corns, the principal differences being in the distribution of palmitic, stearic, and linoleic acids.

Table 8.—Percentage distribution of fatty acids contained in the visceral fat of juvenile and adult hens fed exclusive diets of flight and maintenance chow (FMC), of normal corn, or of high-lysine corn. Values represent the mean of two replicated composite samples of visceral fat from hens in each age-diet group.

Fatty Acids in Visceral Fat	Juvenile Hens			Adult Hens	
	FMC	Normal Corn	High-Lysine Corn	Normal Corn	High-Lysine Corn
Saturated acids					
Lauric (12:0) ^a	1.0	0.9	0.6	0.8	0.5
Myristic (14:0)	0.4	0.3	0.2	0.3	0.2
Palmitic (16:0)	24.2	21.0	21.4	20.5	16.6
Stearic (18:0)	8.2	4.8	5.2	6.2	5.8
Subtotal	33.8	27.0	27.4	27.8	23.1
Unsaturated acids					
Palmitoleic (16:1)	7.4	7.4	6.6	7.7	6.0
Oleic (18:1)	37.8	37.6	39.6	39.1	41.8
Linoleic (18:2)	17.8	27.9	25.8	22.4	28.3
Linolenic (18:3)	1.0	^b	^b	3.0	^b
Arachidonic (20:4)	2.2	^b	0.7	0.1	0.5
Subtotal	66.2	72.9	72.7	72.3	76.6
Total (percentage)	100.0	99.9	100.1	100.1	99.7

^a The numbers preceding and following the colons represent the number of carbon atoms and the number of bonds, respectively.

^b Not isolated in analysis.

ADULT HENS

Body Weight Changes

Adult hen pheasants that were fed either normal corn or high-lysine corn at the restricted rate of 200 g each per week for a 7-week period in late winter and early spring suffered losses in body weight that averaged 5.8 g for those on normal

corn and 65.5 g for those on high-lysine corn (Table 9). Both groups of hens suffered rather drastic losses in weight during the first week of the feeding trial. However, the hens fed normal corn essentially recovered their first-week loss in weight during the subsequent 6 weeks whereas those fed high-lysine corn continued to lose weight throughout the remainder of the feeding trial (Fig. 3).

Table 9.—Body weight statistics for adult hen pheasants fed exclusive diets of 200 g of normal corn or of 200 g of high-lysine corn per hen per week for a 7-week period, March 6–April 24, 1967.

	Mean Body Weight (g) or Weight Change for Specified Diet		F Values _(df)
	Normal Corn (n=6 Hens)	High-Lysine Corn (n=6 Hens)	
Initial weight (March 6)	907.3 ± 40.6*	900.3 ± 22.1	0.02 _{1,10}
Final weight (April 24)	901.5 ± 38.6	834.8 ± 26.3	2.03 _{1,10}
Weight change	−5.8 ± 25.9	−65.5 ± 26.4	2.59 _{1,10}

* Standard errors.

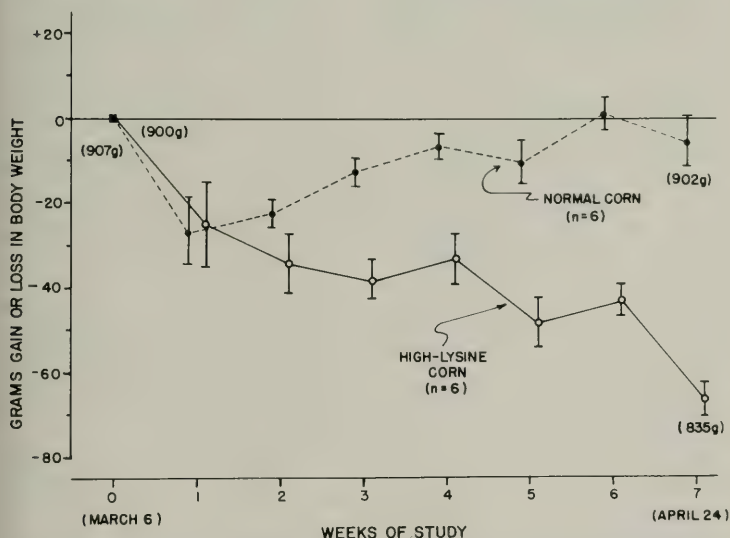


Fig. 3.—Mean change in body weight (g) by weekly periods among adult hen pheasants fed exclusive diets of normal corn or of lysine corn; the vertical lines transecting the means are standard errors. The mean initial and final body weights for each group are given at the left and right of the graph, respectively. Statistically significant ($P < 0.05$; 1 and 10 df) weight changes occurred between diets for only one of the seven successive weekly periods: 2 to 3 ($F = 6.14$).

The changes in body weight recorded for the 7-week period for the six hens in each group were +73, +40, +40, -54, -60, and -68 g for normal corn, and +16, -19, -39, -72, -126, and -153 g for high-lysine corn.

Digestibility Coefficients

With both corn diets restricted to 200 g per hen per week, each hen consumed the total offering, and hence an identical amount of corn. The digestion of the two corns by the adult hens, however, differed significantly, averaging 81.3 percent for normal corn and 76.9 percent for high-lysine corn (Table 10).

Calorie Utilization

The number of calories consumed by the adult hens was similar for the diets of normal corn and high-lysine corn (Table 11). Yet, both the proportionate and absolute utilization of calories differed significantly between the two groups

of hens, being greater for those fed normal corn than for those fed high-lysine corn. The adult hens metabolized 3,921 (84.3 percent) and 3,617 (79.6 percent) kcal per kg of normal corn and high-lysine corn, respectively.

Protein Utilization

The intake of crude protein was similar for the adult hens on each of the two corns because the corns were fed at identical rates and had similar protein contents (Tables 1 and 10). However, both the proportionate and absolute utilization of crude protein by the adult hens differed significantly between the two diets, with the efficiency of protein utilization being greater for hens fed normal corn than for those fed high-lysine corn (Table 10).

Lysine Utilization

The intake of lysine by hens fed high-lysine corn was about 42 percent greater

Table 10.—Comparative utilization of exclusive diets of normal corn and of high-lysine corn, fed at a restricted rate of 200 g per hen per week, by adult hen pheasants for a 7-week period, March 6–April 24, 1967. All values expressed as dry weight.

	Mean Value per Hen per Week for Specified Diet		F Values _(df)
	Normal Corn (n=6 Hens)	High-Lysine Corn (n=6 Hens)	
Food consumed (g) ^a	200	200	
Crude protein ^b consumed (g)	24.0	23.4	
Lysine consumed (g) ^c	0.8	1.1	
Excreta (g) ^d	37.1 ± 0.6 ^e	45.0 ± 1.6	18.85 _{1,10} *
Digestibility coefficient (percent) ^d	81.3 ± 0.2	76.9 ± 0.5	54.07 _{1,10} *
Crude protein in excreta (percent) ^d	47.3 ± 2.1	44.0 ± 2.7	4.24 _{1,10} *
Crude protein utilized (g) ^d	6.3 ± 0.7	3.6 ± 0.7	8.64 _{1,10} *
(percent)	26.3 ± 2.8	15.4 ± 2.9	6.23 _{1,10} *
Change in body weight (g)	-0.8	-9.4	

* Denotes statistical significance, $P < 0.05$. Interactions between weeks yielded no significant F values in any category.

^a Each hen consumed the 200 g of food presented to it each week.

^b See Table 1 for protein content of food.

^c Product of crude protein consumed and amount of lysine in protein.

^d Based on data from Weeks 5 and 7 only.

^e Standard errors.

Table 11.—Comparative utilization of calories by adult hen pheasants fed a restricted diet of 200 g of normal corn or 200 g of high-lysine corn per hen per week for a 7-week period, March 6–April 24, 1967.

	Mean Value per Hen per 7-Week Period for Specified Diet		<i>F</i> Values _(df)
	Normal Corn (n=6 Hens)	High-Lysine Corn (n=6 Hens)	
Calories consumed (kcal)	6,512 ^a	6,362 ^a	
Calories per g excreta ^b	3,925 ± 26 ^c	4,121 ± 28	3,897.40 _{1,10} *
Calories utilized (kcal) ^d	5,492 ± 16	5,066 ± 55	17,095.46 _{1,10} *
(percent) ^b	84.3 ± 0.2	79.6 ± 0.9	27.48 _{1,10} *

* Denotes statistical significance, $P < 0.05$.

^a Each hen consumed the 200 g of food presented to it each week; hence, all hens on each of the two diets consumed the same number of kcal. See Table 1 for caloric content of corns.

^b Caloric values for Weeks 5 and 7.

^c Standard errors.

^d Product of the 7-week consumption of calories and the 2-week (Weeks 5 and 7) percentage utilization of calories for each hen.

than among those hens fed normal corn (Table 12), the difference being attributable to the different proportions of lysine contained in the two corns (Table 1). The difference in proportionate utilization of the lysine between the two corns, although not statistically significant, was slightly greater among hens fed the high-lysine corn. In the final analysis, the adult hens fed high-lysine corn utilized about 33 percent more lysine during the feeding trial than did those hens fed an equivalent amount of normal corn. The response in body weight of the adult hens was not related to the amount of lysine utilized during the 7-week trial ($r = 0.56$, 10 df; $P > 0.05$).

Glands and Organs

Although the adult hens fed normal corn and those fed high-lysine corn exhibited striking differences in the sizes of their organs, glands, and tissue masses (Table 13), none of the differences were statistically significant; there was, however, a pronounced pattern in the differences. Either the mean weight or the percentage of body weight (or both) of sternal muscles, fat strip, visceral fat, liver, ovary (and ovum), oviduct, and thyroids was larger for hens fed normal corn than for those fed high-lysine corn. The parathyroids and adrenals, however, were larger among hens on the high-ly-

Table 12.—Comparative utilization of lysine by adult hen pheasants fed a restricted diet of 200 g of normal corn or 200 g of high-lysine corn per hen per week for a 7-week period, March 6–April 24, 1967.

	Mean Value per Hen per 7-Week Period for Specified Diet		<i>F</i> Values _(df)
	Normal Corn (n=6 Hens)	High-Lysine Corn (n=6 Hens)	
Lysine consumed (g)	5.4 ^a	7.7 ^a	
Lysine utilized (g) ^b	4.6 ± 0.1	6.9 ± 0.2	192.88 _{1,10} *
(percent) ^c	85.4 ± 0.9 ^d	89.0 ± 2.0	2.76 _{1,10} *

* Denotes statistical significance, $P < 0.05$.

^a All hens consumed the 200 g of food presented to them each week; hence, each hen within each dietary group consumed the same amount of lysine.

^b Product of the 7-week consumption of lysine and the 2-week (Weeks 5 and 7) percentage utilization of lysine for each hen.

^c Utilization values for Weeks 5 and 7.

^d Standard errors.

Table 13.—Mean weights of selected tissues, organs, and glands from two groups of adult hen pheasants that were fed, respectively, normal corn or high-lysine corn for a 7-week period, March 6–April 24, 1967. There were no significant differences between paired means ($P > 0.05$; 1 and 10 df),

Tissue Organ, or Gland	Normal Corn (n=6)		High-Lysine Corn (n=6)		Normal Corn		High-Lysine Corn	
	Grams				Percent of Final Body Weight			
Sternal muscles	212.5	± 11.8	205.2	± 4.7	23.5	± 0.6	24.7	± 1.0
Fat strip	2.92	± 0.57	1.46	± 0.45	0.32	± 0.06	0.17	± 0.05
Visceral fat	25.3	± 5.9	13.4	± 4.6	2.79	± 0.63	1.53	± 0.51
Liver	15.0	± 1.2	13.3	± 0.6	1.65	± 0.07	1.60	± 0.08
Ovary	7.6	± 2.8	3.1	± 0.3	0.83	± 0.30	0.37	± 0.03
Largest ovum	2.65	± 1.13	0.70	± 0.21	0.29	± 0.12	0.08	± 0.03
Oviduct	11.6	± 1.4	7.7	± 1.3	1.27	± 0.13	0.93	± 0.16
	Milligrams				Percent (X 10 ⁴)			
Thyroids	64.9	± 11.9	55.8	± 7.3	71.5	± 12.3	66.5	± 7.9
Parathyroids	9.9	± 0.8	12.2	± 2.3	11.1	± 1.2	14.3	± 2.3
Adrenals	93.0	± 4.5	105.5	± 9.1	103.7	± 5.6	126.0	± 9.4

sine diet than among those on the normal corn diet. This pattern of difference in weights of tissues, organs, and glands between the normal corn diet and the high-lysine corn diet for adult hens was nearly the exact opposite of that observed among the juvenile hen pheasants.

Fat and Fatty Acids

The visceral fat from adult hens fed normal corn showed slightly greater amounts of saturated fatty acids and correspondingly lesser amounts of unsaturated fatty acids than did that from hens fed high-lysine corn (Table 8). The ratios of saturated to unsaturated fatty acids in the visceral fat were about 28:72 for the adult hens fed normal corn and 23:77 for those fed high-lysine corn.

DISCUSSION

The 8-week feeding trial with juvenile hen pheasants, which was conducted between mid-October and mid-December, coincided with that period of the year during which wild hen pheasants of comparable ages are gaining in body weight. To illustrate, the body weights of wild juvenile hens captured by nightlighting in east-central Illinois during the 6 years 1956–1961 averaged 833 g ($n=447$) in

October and 943 g ($n=92$) in December (R. F. Labisky, unpublished data), which represented gains of 110 g, or 13.2 percent per hen during the 2 months.

The juvenile hens in the present study posted 2-month changes in mean body weight of +13.8, +3.1, and -1.2 percent on exclusive, ad libitum diets of FMC, high-lysine corn, and normal corn, respectively (Table 2). Wild juvenile hens must supplement their corn-dominated autumn diets with food items more nutritious than corn to post the weight gains that they normally exhibit in autumn. However, as a staple food, high-lysine corn appears to be more favorable than normal corn in supplying the demands for growth by young pheasants, at least when both corns are available in an unrestricted supply.

If not restricted in their food intake, yearling and adult hens usually gain weight throughout late winter and early spring, reaching their maximum weight in April just prior to the onset of egg-laying (Kirkpatrick 1944:178; Breitenbach et al. 1963:25–26; Gates & Woehler 1968:235–238; Anderson 1972:467). The hens in this study, when fed restricted diets of corn during a 7-week span in March and April, averaged weight losses of 0.6 and 7.3 percent on diets of normal

corn and high-lysine corn, respectively; their final body weights averaged 200–300 g below normal weights reported for adult hens at the initiation of egg-laying by Breitenbach (1963:26), Labisky & Jackson (1969:720), and Anderson (1972:459).

Any meaningful discussion of the physiological responses of pheasants to diets of normal corn and high-lysine corn must be prefaced by some knowledge of the nutritional requirements of the species. Unfortunately, data regarding nutritional requirements of pheasants are scarce, particularly for subadult birds, and must be extrapolated from information available for poultry. The National Research Council (1971:15–16) lists the minimum metabolizable energy (ME) requirements for domestic chickens (*Gallus gallus*) and turkeys (*Meleagris gallopavo*) as 2,900–3,095 kcal per kg of food for 14- to 20-week-old birds, and as 2,850 kcal for mature breeders. Thus, the ME obtained by pheasants, both juveniles and adults, from the normal corn and high-lysine corn fed in this study well exceeded the energy levels required by

poultry (Table 14). The FMC, however, only provided growing pheasants 2,837 kcal of ME per kg of ration, slightly less than the minimum ME required by growing poultry. However, Barrett & Bailey (1972:14, 16–17) recently reported that breeding pheasants can perform satisfactorily on diets containing about 2,500 kcal of ME per kg of ration if the protein level is above 13 percent.

The rates of metabolizability of both normal corn and high-lysine corn by juvenile and adult hen pheasants in this study paralleled closely the general 80 percent metabolizability rate of normal corn by chickens (Ewing 1963:83). However, among pheasants, the metabolizability of normal corn was slightly greater than for the high-lysine corn regardless of whether the corns were fed ad libitum to juveniles or in restricted quantities to adults (Tables 3 and 10). Also, juveniles metabolized proportionately more of each of the two corns than did adults, a difference that may have reflected the relative demands of growth.

Our study showed that although the juvenile hen pheasants utilized a similar

Table 14.—Levels of protein, metabolizable energy, and selected amino acids recommended for poultry feeds in relation to quantities supplied in diets fed to pheasants during this study. All levels, except those for metabolizable energy, are expressed as percentages of total diet.

	Dietary Requirements ^a			Foods Supplied 14- to 22-Week-Old Pheasants in This Study		
	Chickens: 14-20 Weeks	Turkeys: 14-20 Weeks	Chickens: Breeders	FMC	Normal Corn	High-Lysine Corn
Crude protein	12.0	16.5	15.0	22.8	12.0	11.7
Metabolizable energy (kcal/kg)	2,900	3,095	2,850	2,837 ^b	3,945 ^b (3,921) ^c	3,808 ^b (3,617) ^c
Selected amino acids						
Arginine	0.72	1.0	0.8	1.42	0.46,0.45 ^d	0.79 ^e
Lysine	0.66	0.9	0.5	1.12	0.38,0.18 ^d	0.55
Methionine	0.24	0.31	0.28	0.32	0.14,0.09 ^d	0.16 ^e
Cystine	0.21	0.21	0.25	0.23	0.14,0.09 ^d	0.20 ^e
Tryptophan	0.12	0.15	0.11	^f	0.09,0.09 ^d	0.15 ^e

^a From National Research Council (1971:15–16); these levels are recommended for achieving satisfactory dietary responses by poultry.

^b ME for juvenile hen pheasants.

^c ME for adult hen pheasants.

^d Amino acids not measured in this particular normal corn (Pioneer 3306). First value, except for lysine, from Cromwell et al. (1967:46) for normal corn containing 9.10 percent protein, and second value from National Research Council (1971:28, 40) for normal corn (No. 2 yellow dent) containing 8.90 percent protein; values are probably conservative as regards Pioneer 3306.

^e Amino acids not measured in high-lysine corn. Value from Cromwell (1967:706) for opaque-2 corn containing 11.60 percent protein.

^f Data not available.

number of calories on all three diets—FMC, normal corn, and high-lysine corn—the proportionate utilization of calories was inversely associated with caloric consumption (Tables 4 and 11). Barrett & Bailey (1972:20), however, reported that breeder pheasants compensated for foods with low ME levels by increasing food consumption, and consequently maintained reasonably similar levels of caloric intake on diets containing from 2,100 to 3,400 kcal of ME per kg. This type of compensatory action did not occur among juvenile hen pheasants fed different diets in our study. The diets of these birds, however, were more variable in ME, protein content, and amino acid patterns than the rations fed by Barrett and Bailey, and hence are not totally comparable.

In our study, the similarity in caloric utilization by juvenile pheasants among the diets characterized by different levels of ME was achieved not by compensatory caloric intake but by compensatory metabolizability. Furthermore, adult hens did not show a greater proportionate utilization of calories from the corn than did juveniles, even though they were fed a restricted ration and consumed fewer calories than they would have consumed on an ad libitum diet of corn.

The National Research Council (1971: 19) listed the dietary protein requirements for starting and growing pheasants at 30 percent. Dale & DeWitt (1958: 292) reported that the growth rates of young pheasants, to 10 weeks of age, were less on diets containing 15, 18, and 22 percent protein than on diets containing 28 percent protein. The Council (1971:15-16) also listed the protein requirements of the chicken as 20-23 percent for chicks, 12-16 percent for growing chickens, and 15 percent for laying (breeding) chickens; comparable levels for domestic turkeys were 28, 14-20, and 14 percent, respectively. The reported protein content in the diets of wild hen pheasants in the Midwest ranged seasonally from a minimum of about 12 percent

to a maximum of about 19 percent (Korschgen 1964:169, 174). Collectively, these findings suggest that the protein needs of pheasants are probably satisfactorily met at levels of 16-20 percent for juveniles older than 14 weeks and 15 percent for adult breeders. Therefore, in this study, the dietary protein levels for pheasants were sufficient in the FMC (22.9 percent), but insufficient in both normal corn (12.0 percent) and high-lysine corn (11.7 percent).

Whereas consumption of crude protein by the juvenile hen pheasants differed among birds fed FMC, normal corn, and high-lysine corn (Table 3), the proportionate utilization of the protein consumed, irrespective of amount, was similar on all diets. Thus, among juvenile pheasants the total amount of protein utilized was related directly to the amount consumed—a situation opposite that for caloric utilization.

Although adult hens consumed similar amounts of protein from the two corns, which were fed at a restricted rate, they utilized 41 percent less of the protein from high-lysine corn than from normal corn (Table 10). Thus, although both corns yielded dietary protein levels that were unsatisfactory to juveniles and adults, the pheasants still failed to utilize about three-fourths of all the protein they consumed in corn.

Eleven of the 23 verified amino acids in proteins are essential to birds; that is, they cannot be sufficiently synthesized by the bird and must be taken in via the diet. Ewing (1963:201, 203) points out that arginine, lysine, methionine, cystine, and tryptophan are particularly important to birds because they are essential amino acids that are in critical demand during avian growth and development; the other amino acids are either synthesized by the bird or are present in ample quantities in most foods.

Important to the understanding of the amino acid complex is the fact that a deficiency of any essential amino acid will not only reduce the utilization of other

amino acids, but will also reduce the utilization of the entire diet. Thus, although this paper is concerned principally with the growth-associated amino acid, lysine, other amino acids that are potentially important to pheasants cannot be ignored. The FMC ration provided to pheasants in this study offered adequate quantities of protein and the essential amino acids for both subadult and adult birds (Table 14). The normal corn and high-lysine corn diets, while providing minimal amounts of protein, did not supply adequate quantities of amino acids. The amino acids most lacking in the corns were lysine and methionine. High-lysine corn, however, offered an amino acid profile superior to that of normal corn, and the profiles of both corns were more aligned with the requirements of adult birds than of growing pheasants.

The importance of lysine to growth was well illustrated in a study by Baldini et al. (1953:946-948). They demonstrated that young bobwhites (*Colinus virginianus*), which reportedly required diets with 28 percent protein, could survive and grow well on diets containing as little as 20 percent protein as long as the diets contained adequate amounts of lysine. In their experiments, the addition of 0.3 percent lysine to a base diet of 20 percent protein and 1.0 percent lysine produced a ration with growth and survival qualities for bobwhites that were equal to those provided by a diet containing 28 percent protein and 1.0 percent lysine; thus, 0.3 percent lysine essentially replaced 8.0 percent crude protein. Such findings offer support for our conclusion that the amount of lysine utilized by juvenile pheasants contributed more significantly to their growth than did the amount of crude protein utilized (Table 6).

As with crude protein, pheasants exhibited no compensatory utilization of lysine; the utilization of lysine was related directly to its intake for both juvenile and adult birds (Tables 5 and 12). Perhaps the most interesting observation was the

extremely high utilization (99.2 percent) of lysine from high-lysine corn by juvenile pheasants. This rate of utilization was not maintained by adult hens.

The role of inadequate nutrition—quantitative or qualitative—as regards the physiology of stress in vertebrates is poorly understood. Among mammals, the term “stress” has become almost synonymous with increased adrenocortical activity (see review by Christian 1963). Presumably, some adverse stimulus triggers, via the hypothalamus, an increased release of adrenocorticotrophic hormone (ACTH), which in turn results in the increased production and secretion of corticosteroids from the adrenal cortex that are necessary for maintaining physiological homeostasis under the given stress. (Prolonged exposure by the animal to an adverse stimulus may result in exhaustion of the adrenal cortex, the subsequent failure of corticosteroid production, and finally death.) To produce the additional corticosteroids, the adrenal cortex undergoes hyperplasia and hypertrophy—hence, enlargement of the gland. Thus, enlarged adrenals have become generally recognized as clinical evidence of acute or chronic distress in mammals.

Whether enlarged adrenals are a measure of stress in birds is not clear. Like Christian & Davis (1966:11-13), who found a direct relationship between adrenal size (of mature females) and population density for vole (*Microtus pennsylvanicus*) (Neave & Wright 1968: 634) reported a positive correlation between adrenal-weight indices and population density for ruffed grouse (*Bonasa umbellus*). Breitenbach et al. (1963:34) reported that the adrenals of adult hen pheasants that were restricted in their food intake (45 g per day) did not hypertrophy; however, the adrenals of individual hens, in noticeably poor condition, exhibited a marked increase in size. Also, Newlon et al. (1964:538-539) observed that the adrenal weights of bobwhites were greatest for birds fed those foods which yielded the poorest perform-

ance in maintaining body weight. These observations, coupled with our findings that the adrenal weights of hen pheasants were inversely related to changes in body weight (Table 7 and 13; Fig. 1-3), suggest to us that enlarged adrenals offer diagnostic symptoms of the stresses of inadequate nutrition in pheasants, and possibly other birds.

The deposition and mobilization of depot fats are dynamic processes—even in an animal in reasonably stable energy balance (White et al. 1968:500). We found that depot fat, both strip and visceral, was greatest for juvenile hen pheasants fed high-lysine corn, intermediate for those fed FMC, and least for those fed normal corn (Table 7). In contrast, adult hens, fed restricted but equal amounts of the two corns, accumulated greater fat deposits on a diet of normal corn than on a diet of high-lysine corn (Table 13). The fat deposits from these adult hens, irrespective of the type of corn diet, were many times smaller than those reported in spring for confined hens fed a high-protein ration ad libitum (Breitenbach 1963:32) or for wild hens (Anderson 1972:461). Breitenbach et al. (1963:34) presented evidence that the storage of fat may be stimulated by increased amounts of adrenocorticosteroids. Hence, if the production of corticosteroids paralleled increased adrenal size, as would be expected, fat deposits should have been related directly to adrenal size. We did not observe this relationship among the hens in this study. The birds' depot fats, which represent their largest reservoir of energy, were related to body weight, and therefore inversely reflected the hens' day-to-day energy demands.

Depot fat consists chiefly of triglycerides; fatty acids, both saturated and unsaturated, are hydrolyzed from triglycerides via the action of the lipases. We found that the ratios of saturated to unsaturated fatty acids in the visceral fat from juvenile and adult hen pheasants fed normal corn and from juvenile hens

fed high-lysine corn were about 27:73 (Table 8). Correspondingly, normal corn and high-lysine corn contained saturated to unsaturated fatty acid ratios of 14:86 and 19:81, respectively (Table 1). Hence, there was some disparity in the distribution of saturated and unsaturated fatty acids between the depot fat of pheasants and their corn diets. Although the distribution of fatty acids in the depot fat of herbivorous galliform birds generally reflects the composition of the diet (Moss & Lough 1968:559; West & Meng 1968b:438), West & Meng (1968a:539) have also provided evidence that, at least for the redpoll (*Acanthis flammea*), environmental conditions and the physiological state of the bird also influence the fatty acid composition of the visceral fat.

Interestingly, the ratio of saturated to unsaturated fatty acids in the visceral fat of the adult hens fed the restricted intake of high-lysine corn was 23:77, which represented an increase in unsaturated fatty acids over the 27:73 ratio recorded for juvenile hens fed either high-lysine corn or normal corn ad libitum and for adult hens fed the restricted diet of normal corn. The shift by adult hens fed high-lysine corn to a fatty acid composition of depot fat that more closely reflected that of their high-lysine corn diet is not surprising because White et al. (1968:499) reported that fatty acid profiles of depot fat resemble the dietary profiles more closely when the depot fat is being depleted. The adult hens fed high-lysine corn at the restricted rate were decreasing in body weight, and therefore probably drawing on the stores of saturated fatty acids for reserve energy. Under these conditions the replacement fatty acids reflected the high proportion of unsaturates in the high-lysine corn diet.

Plant seeds abound in unsaturated fatty acids. The principal unsaturated fatty acids in the corns were oleic and linoleic. Correspondingly, the principal fatty acids in the visceral fat of pheasants were oleic and linoleic (Table 8); however, the samples of visceral fat contained pro-

portionally more oleic acid and considerably less linoleic acid than either of the corns. Linoleic was the principal fatty acid in the depot fats of the heather-eating red grouse (*Lagopus lagopus scoticus*) (Moss & Lough 1968:560-561) and of the willow-eating willow ptarmigan (*Lagopus lagopus alascensis*) (West & Meng 1968b:438). However, as we found for the pheasant, Walker (1964:63-64) reported the predominant fatty acid in the depot fat of the seed-eating bobolink (*Dolichonyx oryzivorus*) to be oleic acid. Oleic acid and linoleic acid seem to be the principal unsaturated fatty acids that characterize the depot fats of granivorous and herbivorous birds, respectively.

The parathyroid glands secrete a hormone that functions importantly as a regulator of calcium, and probably phosphorus, metabolism; high and low levels of circulating calcium act on the glands to inhibit or stimulate, respectively, secretion of the parathyroid hormone (Geschwind 1961:434-436). Hypertrophied parathyroid glands and reduced levels of blood calcium are characteristic responses of laying chickens to low-calcium diets (Bloom et al. 1960:207). In our study, we fed juvenile hen pheasants diets that ranged from about 14,000 ppm calcium for FMC to about 40 ppm calcium for the corns (Table 1); corns in general are notoriously low in calcium content. The parathyroids from these juvenile hens fed normal corn and high-lysine corn weighed at least twice as much as the glands from those fed FMC (Table 7), and nearly twice as much as the glands from their wild counterparts (Anderson 1972:485). Furthermore, the adult hens fed exclusive diets of the corns during late winter and early spring (Table 13) had parathyroids substantially larger than those reported by Anderson (1972:485) for wild adult hens at a comparable time of the year. The hypertrophied parathyroid glands from hen pheasants fed exclusive diets of calcium-deficient corns constituted strong clinical evidence that the birds were suffering from a negative calcium balance.

The gonadal recrudescence among pheasants in spring is a response, mediated via the hypothalamo-hypophyseal axis, to increasing photoperiod (Bissonnette & Cseh 1936:106; Hiatt & Fisher 1947:538, 543; Greeley & Meyer 1953:353-354). In Illinois, complete gametogenesis among hens, as evidenced by egg-laying, is attained between late March and mid-April (Labisky & Jackson 1966:382; Labisky 1968:69; Labisky & Jackson 1969:719). In our study, none of the adult hens fed corn diets restricted to an intake of 200 g per week had initiated egg-laying at the conclusion of the experiment on April 24. Furthermore, the reproductive tracts of these hens, when compared to hens on unrestricted diets or in the wild (Breitenbach et al. 1963:29; Anderson 1972:484) were severely underdeveloped physiologically for late April. The lag in ovarian and oviducal development was more pronounced for hens fed high-lysine corn than for those fed normal corn (Table 13).

The findings from this and previous investigations of confined pheasants (Gerstell 1942:68; Kozlik 1949:62; Breitenbach et al. 1963:27; Gates & Woehler 1968:240) have demonstrated that delays in egg-laying are related to poor physical condition in spring; Edwards et al. (1964:278) hypothesized a similar situation for wild pheasants. Also, poor physical condition, usually the result of malnutrition, signifies reduced reserves of energy. Fisher (1967:121) cited evidence to show that domestic hens would cease egg production as soon as their protein reserves were exhausted after being placed on a protein- or amino acid-deficient diet. Corns do not abound in protein, and are deficient in one or more of the essential amino acids.

The inhibitory effects of inadequate nutrition on reproduction in galliform birds, however, seem to be mediated through the hypothalamo-hypophyseal axis and not directly by protein or amino acid imbalances. Morris & Nalbandov (1961:687) demonstrated that undernourished or starved domestic pul-

lets failed to produce sufficient gonadotropins to promote functional ovarian and oviducal development. Gates & Woehler (1968:243) sum it up aptly: "It would appear that restoration of body condition [in pheasants] . . . is a requisite for recrudescence, normal rates of egg laying being delayed until energy is available for reproduction and the secretory integrity of the pituitary is restored."

The nutritional responses of pheasants to normal corn and high-lysine corn are not consistent for birds of different ages. The weight gains and physiological parameters for juvenile hen pheasants fed high-lysine corn in autumn were distinctly more favorable than for those correspondingly fed normal corn. Yet adult hens fared far better on normal corn as an emergency food in late winter than they did on high-lysine corn. Thus, although potentially of benefit to growing pheasants, high-lysine corn may well be a detriment to mature pheasants. These conflicting results are at least partially explainable. The greater nutritional value to young pheasants of high-lysine corn, when contrasted with normal corn, undoubtedly lies in its higher content of the growth-oriented amino acid, lysine. Our findings indicated strongly that the weight gains of juvenile pheasants were dependent directly on the amount of lysine utilized. Evidence in support of these findings is provided by the research of Cromwell et al. (1967:711), who studied the nutritional responses of domestic chicks to the two corns: ". . . the beneficial effects of *opaque-2* corn over normal corn appeared to be mediated solely through its higher lysine content." These workers, however, fed the corns as a part of nutritionally balanced basal diets, and not as exclusive food items. They also pointed out (p. 712) that the beneficial responses exhibited by young animals to *opaque-2* corn would probably be much less for mature animals that have a lower protein requirement. Furthermore, the probability of selecting

genetically for a pheasant that responds to higher than normal dietary levels of lysine by exhibiting an improved rate of growth seems remote, as Godfrey (1968:1565) found that the heritability for lysine utilization among Japanese quail (*Coturnix coturnix japonica*) was very low. Thus *opaque-2* corn apparently is not a panacea for assuring adequate nutrition in pheasants. Another modified-protein corn called *floury-2*, which contains higher concentrations of both lysine and methionine than those in most other corns (Nelson et al. 1965:1470; Cromwell et al. 1968:846), may offer nutritional benefits for birds that are potentially superior to those provided by either normal corn or *opaque-2* corn.

Corn, an important food source to many species of wildlife, is a nutritive staple for pheasants. To illustrate, Newlon et al. (1964:536-537), in evaluating foods for sustaining bobwhites, reported that the mean survival duration for juvenile and adult birds fed an exclusive, ad libitum diet of normal corn in November was 22.6 days; no bobwhite survived the 38-day feeding trial. As observed in this study, however, exclusive ad libitum diets of normal corn sustained juvenile pheasants, with only minor weight losses, for 8 weeks in autumn without any mortality. Also, adult hens fed a restricted intake of normal corn (200 g per week) in late winter and early spring maintained their body weights for a 7-week feeding trial. If, however, pheasants are to parallel the annual cycle of body weights that normally characterize thriving populations in the wild they must supplement their corn-dominated diets with food items more nutritiously balanced than high-lysine or normal corn. A plausible hypothesis, therefore, is that the high rates of nonhunting mortality observed among wild juvenile pheasants in Illinois during autumn (R. F. Labisky, unpublished data) may be directly or indirectly related to nutritive imbalances resulting from the surging availability of waste corn in the birds' diet.

SUMMARY

Corn is an important food for many wild animals and is especially prominent in the diet of wild pheasants in the United States. Yet despite its importance as a staple food of pheasants, knowledge of its nutritional value to the species is still quite limited. In 1963, scientists added another dimension to corn nutrition by discovering a modified-protein corn, *opaque-2* corn (herein called high-lysine corn), which has substantially greater amounts of lysine in its endosperm than does normal corn. Lysine is one of the essential growth-promoting amino acids.

The objectives of this investigation were to ascertain the physiological responses of juvenile hen pheasants in autumn, and of adult hens in late winter and early spring to exclusive diets of normal corn and high-lysine corn. In the 8-week feeding trial for juveniles, October 20–December 15, 1966, 21 hens in three groups of 7 each were fed exclusive, ad libitum, diets of a balanced ration (FMC), normal corn, or high-lysine corn. Analyses of the three foods yielded the following: FMC—4.28 kcal per g, 22.8 percent protein, and 4.9 percent lysine in protein; normal corn—4.65 kcal per g, 12.0 percent protein, and 3.2 percent lysine in protein; and high-lysine corn—4.54 kcal per g, 11.7 percent protein, and 4.7 percent lysine in protein. The feeding trial for juveniles coincided with the season in which juvenile hens, in contrast to adult hens, suffer disproportionately high rates of nonhunting mortality in Illinois, and also simultaneously with the time that waste corn from the harvest suddenly becomes an abundant food source. Hence this phase of the study was designed partially to determine if juvenile mortality among wild pheasants was related to unbalanced nutrition. In the 7-week feeding trial for adult hens, March 6–April 24, 1967, 12 hens in two groups of 6 each were fed exclusive diets of normal corn or high-lysine corn at the restricted rate of 200

g per bird per week. This restricted intake of food was intended to simulate the conditions that wild hens in the Midwest often confront in late winter and early spring.

The juvenile hen pheasants fed exclusive diets of FMC and high-lysine corn for the 8-week period in autumn posted gains in body weight that averaged 98.4 g (13.8 percent) and 23.4 g (3.1 percent), respectively; correspondingly those juvenile hens fed normal corn suffered average losses of 8.7 g (1.2 percent). Wild juvenile hens averaged gains of 110 g (13.2 percent) for the comparable autumn period.

Adult hens, each fed a restricted intake of 200 g of corn per week for the 7-week period in late winter and early spring, averaged losses in body weight of 5.8 g (0.6 percent) for normal corn and 65.5 g (7.3 percent) for high-lysine corn. Whereas hen pheasants usually exhibit gains in body weight in late winter, reaching their maximum weight just prior to the onset of egg-laying (usually in April), the adult hens on the restricted intake of corn averaged 200–300 g below the normal body weights of wild hens in April.

The kcal of energy metabolized per kg of food consumed by juvenile hens was 2,837 (66.3 percent efficiency) for FMC, 3,945 (84.8 percent) for normal corn, and 3,808 (83.3 percent) for high-lysine corn; adult hens metabolized 3,921 kcal per kg (84.3 percent) of normal corn and 3,617 kcal per kg (79.6 percent) of high-lysine corn. Juvenile hens, despite the differences in the yield of metabolizable energy among the foods, utilized the same number of calories on all three diets; the similarity in caloric utilization was achieved by compensatory metabolizability and not by compensatory caloric intake.

Unlike the situation for calories, hen pheasants exhibited no compensatory utilization of either crude protein or lysine. The total amounts of both protein and lysine utilized by hen pheasants

were related directly to dietary intake. Even though the dietary protein levels of both corns were unsatisfactory, the birds utilized only about one-fourth of the protein they consumed. The proportionate utilization of lysine by either adult or juvenile hens exceeded 85 percent for all diets. Interestingly, juvenile hens utilized 99 percent of the lysine consumed from high-lysine corn—a rate not achieved by adult hens. Most important was the finding that the body weights of juvenile pheasants in autumn were more dependent on the amount of lysine utilized than on the amount of crude protein utilized.

The adrenal weights of hen pheasants were inversely related to changes in body weight, which in turn was a reflection of the consumption of diets of different nutritional offerings. These findings indicated that enlarged adrenal glands in pheasants, and possibly other avian species, may offer diagnostic evidence for detecting the physiological stresses of unbalanced or inadequate nutrition.

Depot fats of hen pheasants were directly related to changing body weight, a relationship that reflected changing demands for energy for growth or maintenance. The ratio of saturated: unsaturated fatty acids in the visceral fat of hens fed corn was about 1:3, which was greater than that found in the corns. Oleic and linoleic were the principal fatty acids in corn, and, correspondingly, the most prominent in the depot fats of pheasants.

Hypertrophied parathyroid glands from hen pheasants fed exclusive diets of calcium-deficient corns offered strong clinical evidence that wild hen pheasants

on corn-dominated diets would suffer from a negative calcium balance.

The reproductive tracts of adult hen pheasants fed restricted diets of normal corn or high-lysine corn, unlike those of wild hens or hens fed unrestricted diets, were severely underdeveloped in late April. The lag in ovarian and oviducal development was substantially greater for hens fed high-lysine corn than for those hens fed normal corn. The effects of inadequate nutrition are apparently mediated through the hypothalamo-hypophyseal-gonadal axis.

The nutritional responses of young and adult hen pheasants to normal corn and high-lysine corn were not similar. The physiological profiles of juvenile hens fed high-lysine corn in autumn were distinctly more favorable than of those fed normal corn. The greater nutritional value to young pheasants of high-lysine corn, in contrast to normal corn, very likely is associated with its higher content of lysine, an essential growth-promoting amino acid. However, as an emergency food for adult hens in late winter or early spring, normal corn proved superior to high-lysine corn.

To attain the physiological plateaus that normally characterize self-maintaining populations in the wild, pheasants must supplement their corn-dominated diets with foods more nutritiously balanced than corn—high-lysine corn not excepted. Dietary imbalances, resulting from the surging availability of waste grain from the corn harvest, may be associated with the high rates of non-hunting mortality among juvenile hen pheasants in Illinois during autumn.

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Frontispiece.—These before and after pictures along the Broadwalk on the University of Illinois campus illustrate vividly how a cathedral-like archway of stately American elms can be destroyed quickly and completely by phloem necrosis and Dutch elm disease. The upper photograph was taken in September 1954. The lower photograph was taken in September 1966, several years after the university had begun replacing the elms with other species. (Upper photo by W. E. Clark; lower photo by W. D. Zehr)

An Urban Epiphytotic of Phloem Necrosis and Dutch Elm Disease, 1944–1972

J. Cedric Carter

Lucile Rogers Carter

THE AMERICAN ELM was used more extensively than any other species as a shade tree in Illinois prior to 1940. It was especially valued for its rapid growth, majestic size, vase shape, and extensive shade. It was used for streets, boulevards, and park drives, as well as in lawns. In many cities throughout the state it represented half or more of the shade trees lining the streets. In some cities it was estimated that three-fourths of the shade trees were American elms. Because of the loss to diseases of millions of elms, especially American elms, since 1940, most cities and homeowners now plant other trees. The elm problem has made many people aware of the importance of using diversified plantings to avoid such a catastrophe in the future.

Extensive dying of elms in central Illinois, especially in Bloomington, Normal, and Champaign, occurred as early as 1883 (Forbes 1885:112; 1912:3). This dying of elms subsided within a few years. Although the cause of the elm deaths was not determined, the symptoms reported are not typical of any current vascular wilt disease.

In 1907 elms were reported dying in southern Illinois and around Fairfield in Wayne County. By 1912 numerous elms were dying in 14 towns (Cairo, Carbondale, Centralia, Clayton, Du Quoin, Edwardsville, Fairfield, Galatia, McLeansboro, Mt. Vernon, Quincy, Robinson, Sumner, and Vandalia) in 13 counties in southern and western Illinois (Forbes 1912:5). Careful examination of affected trees revealed that although the small fibrous roots were dead, some of the main roots were alive, as were some of the leaves. This early dying of elms was generally

referred to as "elm blight" and attributed to various conditions and agencies, including drought, exhaustion of soil nutrients, insect attack (borers and bark beetles), and diseases of unknown causes (Forbes 1912:7–10).

Following 1912 no reports of extensive dying of elms appeared until 1930, when many elms were killed in and near several large and small cities, notably Hillsboro in south-central Illinois, Danville in east-central Illinois, Peoria in north-central Illinois, Quincy in west-central Illinois, and Cairo at the southern tip of the state (Carter 1945:23). By 1940 (Carter 1954) elms were dying throughout the southern half of the state and as far north as Danville on the east and Quincy on the west. Other towns on the northern border of this area included Charleston, Shelbyville, Taylorville, and Pittsfield. The greatest number of affected trees were in a broad belt extending diagonally southwestward from Danville and Paris on the east to Alton and Belleville on the west. This area is north of the southern part of the state where heavy losses of elms occurred earlier. This dying of elms continued to spread northward to Urbana in 1944, to Mattoon, Springfield, and Lincoln in 1945, and to Decatur, Bloomington, and the area around Burlington, Iowa, in 1948. General and widespread dying of elms became stabilized by 1948 with the northern boundary of the affected area represented by a line extending from Danville on the east through Champaign-Urbana, Bloomington, and Peoria to the area around Burlington, Iowa, on the west. North of this area dying elms were found in only six cities — Melvin

and Dwight in 1945, Rockford in 1946, Chebanse in 1950, and Chenoa and Onarga in 1953.

Following the 1938 report that a disease of a virus nature was killing elms in Ohio (Swingle 1938), it was soon determined that the widespread dying of elms in the Ohio Valley region of the Midwest was caused by the same disease. It was determined to be a virus disease called phloem necrosis (Swingle 1940 and 1942). However, recent work by Wilson et al. (1972) indicates that elm phloem necrosis may be caused by a mycoplasma-like organism (MLO).

The symptoms exhibited by dying elms in Illinois as early as 1912 were typical of those described later for phloem necrosis. It appears that this disease was the major cause of elms dying in southern Illinois from 1907 to 1950.

Dutch elm disease, caused by *Ceratocystis ulmi* (Buism.) C. Moreau, was discovered in one American elm in Coles County (east-central Illinois) in 1950, and the disease spread rapidly, especially in the area where elm phloem necrosis was killing thousands of elms annually. By 1969 it had spread into all 102 counties of the state. At present each disease kills many elms annually, phloem necrosis in the southern two-thirds of the state and Dutch elm disease throughout the state.

The first symptom of phloem necrosis is the dying of fibrous roots. This symptom is followed by foliage symptoms, which appear as drooping leaf blades and upward curling leaf margins. Next the leaves turn yellow, brown, or both, and drop from the tree. These symptoms may occur over one or more growing seasons. On some trees the foliage wilts rapidly within a few weeks and turns brown, but many leaves remain attached to the branches. Occasionally a tree may have one or a few large branches dying simultaneously over a period of 1 or more years.

The infection of individual branches by the Dutch elm disease fungus re-

sults in wilting and dying foliage on the affected branches. Frequently, the early symptom of Dutch elm disease is wilting foliage on one or a few branches. Wilt of the entire tree occurs after the fungus becomes systemic in the tree. The yellowing of leaves over the entire crown is uncommon in Dutch elm disease but common in phloem necrosis.

The present study was initiated, following the appearance of phloem necrosis in Urbana in 1944, to obtain data on the number of elms affected annually by the disease and to study the pattern of spread in a municipal area where no city-wide control program was practiced. With the appearance of Dutch elm disease in Urbana in 1951, the study was expanded to include both diseases and the relationship of the two diseases in a municipal area.

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The photograph for Fig. 9 was taken by William Clark, formerly Natural History Survey Photographer. All other illustrations, except as noted, were photographed by Wilmer Zehr, Survey Photographer. The illustrations in Fig. 5, 7, 8, 10, 11, and 12 were prepared by Lloyd LeMere, Survey Illustrator.

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LITERATURE REVIEW

Field-grown elms do not show symptoms of phloem necrosis for 1 or more years following the introduction of the MLO (Baker 1949:729, 730; Campana 1958). Elms affected by this disease usually die during the growing season in which symptoms first appear. However, some elms may show symptoms for two or sometimes three growing seasons before dying (Campana 1958; Swingle 1938:757). Phloem necrosis affects only the American elm (*Ulmus americana* L.) and its cultivars and the winged elm (*U. alata* Michx.). The phloem necrosis MLO is carried by the elm leafhopper (*Scaphoideus luteolus* Van D.). The MLO is introduced into the leaves of healthy elms by the feeding activity of elm leafhoppers that have previously fed on leaves of phloem necrosis-affected elms.

Elms affected by Dutch elm disease may die during the growing season when symptoms first appear, or they may die during the following growing season. Occasionally an affected elm may not die until the third growing season (Banfield, Rex, & May 1947). Dutch elm disease affects all elm species, but the Asiatic species are relatively resistant (Bretz, Swingle, & Parker 1945). The American elm appears to be more susceptible than the other native and European species (Neely & Carter 1965).

Published data on the loss of elms in municipal areas where both diseases occur are limited. However, data are available on losses caused by each disease in areas where only one was present (Campana & Carter 1955 and 1957; Carter 1954, 1955, and 1961; Neely, Carter, & Campana 1960; Neely 1967).

In municipal plantings of elms, losses resulting from phloem necrosis may increase from a few scattered trees when the disease is first discovered to several hundred trees annually within 3 years. In three municipalities in central Illinois the number of phloem

necrosis-affected elms increased from 9 in 1945 to 370 in 1948 in Lincoln, from 5 in 1945 to 417 in 1948 in Mattoon (Carter 1950:50), and from 6 in 1948 to 154 in 1951 in Bloomington.¹ In Mt. Pulaski, which had approximately 600 elms in 1942 when phloem necrosis was first found there, all but 19 elms were killed by the disease by 1948 (J. C. Carter, unpublished data).

Phloem necrosis also kills elms in rural areas. In a survey made in southern Illinois in 1945, the numbers of elms recorded as dying from phloem necrosis were 1,644 in rural areas and 1,655 in municipal areas (Carter 1954).

In municipal plantings of elms, Dutch elm disease losses may increase from a few scattered trees when the disease is first discovered to hundreds of trees each year in a few years. In five municipalities in northern Illinois where Dutch elm disease was discovered in 1955 and where phloem necrosis was not present, the total numbers of diseased elms from 1955 through 1961 were over 4,400 in Aurora, 1,600 in Elgin, 2,500 in Joliet, 1,400 in Waukegan, and 1,000 in Zion. The percentages of the original elm populations that became diseased in these five cities during this period were 48, 23, 33, 11, and 27, respectively (Neely 1967: 513). In Bloomington in north-central Illinois, Dutch elm disease was first found affecting 10 elms in 1954 following a 6-year period in which 932 elms were affected by phloem necrosis. The number of elms affected annually by Dutch elm disease increased to 242 in 1955 and to 507 in 1956 (Campana & Carter 1957: 636).

In areas where both diseases are present, the incidence of phloem necrosis results in an increase in the occurrence of Dutch elm disease (Campana & Carter 1955). The native elm bark beetle (*Hylurgopinus rufipes* Eichh.) and the smaller European elm

¹ The data on the loss of elms in Bloomington were obtained by annual surveys made by the senior author.

bark beetle (*Scolytus multistriatus* Marsh.), vectors of the Dutch elm disease fungus, colonize and overwinter in the bark of weakened, dying, and recently killed elms, including those affected by phloem necrosis.

The incidence of Dutch elm disease does not increase the occurrence of phloem necrosis (Campana 1958). Elms killed by either disease and left standing are not colonized by the elm leafhopper (*S. luteolus* Van D.), vector of the phloem necrosis MLO. This insect overwinters in the egg stage. The eggs are embedded in the soft cork parenchyma of elm bark (Baker 1949: 731).

Dutch elm disease may not only obscure the presence of phloem necrosis, but it may kill phloem necrosis-affected trees before external symptoms of phloem necrosis become apparent (Campana & Carter 1957; Campana 1958). The rate of increase of Dutch elm disease exceeds that of phloem necrosis in areas where Dutch elm disease appears after phloem necrosis has been present for several years (Campana & Carter 1957:639; Carter 1955:36-37; Neely, Carter, & Campana 1960:167, 169).

Phloem necrosis-affected elms colonized by smaller European elm bark beetles infested with the Dutch elm disease fungus will harbor that fungus. Of 40 such trees examined in Urbana in 1952, 8 contained the Dutch elm disease fungus (Campana 1954:358).² Populations of the smaller European elm bark beetle increase rapidly in areas where dying and recently killed elms are present. This situation was common in the 1950's in the southern two-thirds of Illinois where thousands of elms killed annually by phloem necrosis were not removed immediately upon discovery of the disease (Campana 1954).

When symptoms of both diseases occur in one elm, infection by the phloem necrosis MLO most likely occurs first, since the MLO is in the tree 1 year or more before symptoms of phloem necrosis become apparent (Baker 1948 and 1949:729, 730; Campana 1958; Swingle 1938). Therefore, elms showing early symptoms of phloem necrosis may show symptoms of Dutch elm disease later in the same year or in the following year before they die. Elms infected by the phloem necrosis MLO and the Dutch elm disease fungus in the same year may show symptoms of Dutch elm disease in that year, but not symptoms of phloem necrosis.

Some of the data presented in this bulletin on the loss of elms from phloem necrosis and Dutch elm disease in Champaign and Urbana have been reported previously (Campana & Carter 1955 and 1957; Carter 1955; Neely, Carter, & Campana 1960).

MATERIALS AND METHODS

The twin cities of Champaign and Urbana represent a contiguous municipal area with a common boundary. This area is approximately 5 miles [8 km] east and west and 2.5 miles [4 km] north and south. It is traversed by approximately 200 miles [320 km] of streets, mostly lined with trees on each side and with additional trees in lawns.

In 1950 all elms and all other species of trees were counted in 75 city blocks to obtain an estimate of the entire tree population as well as the elm population. To obtain the estimate, the entire tree population was divided into 25 areas. The areas were selected so that each area included elms of a given size and age. The sizes of trees counted varied from approximately 4 to 20 inches [100-500 mm] in trunk diameter and 20-75 feet [6-23 m] in height. Most of the larger elms were present in the older residential areas.

All trees were counted in each of three blocks selected at random in each

² Data originally gathered by E. B. Himelick, Illinois Natural History Survey, and published by Campana.

of the 25 areas. From the data obtained (Table 1) it was estimated that there were 12,195 elms in the municipal study area. The data also showed that the tree population was composed of 51 percent elms and 49 percent other species. An estimated 2,000 elms in Crystal Lake Park in the north part of Urbana were later included in the total elm population, bringing to 14,195 the estimated number of elms in the

Table 1.—Estimated tree population in Champaign-Urbana, Illinois, in 1950.

City	Elms		Other Species	
	Num- ber	Per- cent	Num- ber	Per- cent
Urbana	4,235	51.8	3,946	48.2
Champaign	7,960	50.6	7,775	49.4
Total or percent	12,195	51.0	11,721	49.0

twin-city area. The actual number of elms recorded during this 29-year study was 14,103. Of these elms, 66 percent were on public property and 34 percent on private property. The distance between elms along many streets was 30 feet [9 m] or less. This close spacing was common in blocks and along streets planted almost exclusively to elms. Some lots with frontages of about 50 feet [15 m] in residential areas had two elms on the parkway and one or more elms on the front lawn.

The elms under observation included all American and European species of elms that could be observed from the street on public and private property within the confines of Champaign and Urbana. In addition to the American elm and its cultivar, the Moline elm, there were 25 slippery elms and 9



Fig. 1.—Phloem necrosis symptoms. The tree on the left shows typical symptoms of phloem necrosis in contrast to the healthy tree on the right. Phloem necrosis is indicated by the cupping or rolling and yellowing of foliage over the entire tree crown. (Photo by J. C. Carter)

English elms. Asiatic species were not included, as they are immune to phloem necrosis and resistant to Dutch elm disease. The elms on the University of Illinois campus were sprayed for 5

years to control phloem necrosis, and therefore they were not included in this study.

Elms removed from the study area but not affected by phloem necrosis or

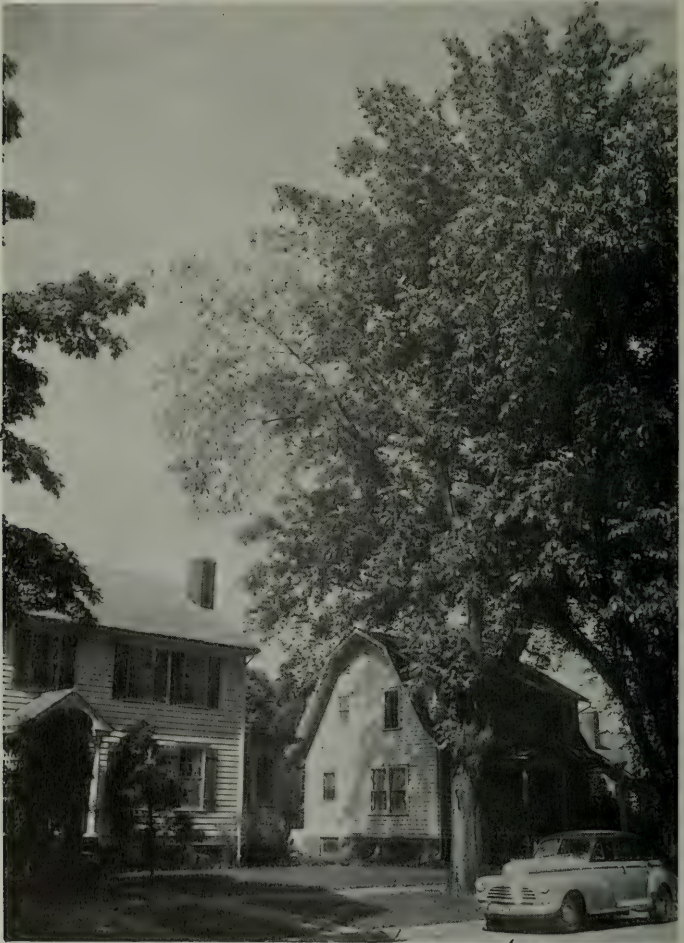


Fig. 2.—Dutch elm disease symptoms. Dutch elm disease frequently appears as wilting and browning of foliage on one or a few branches. This tree has foliage wilting on the left major branch. (Photo by J. C. Carter)

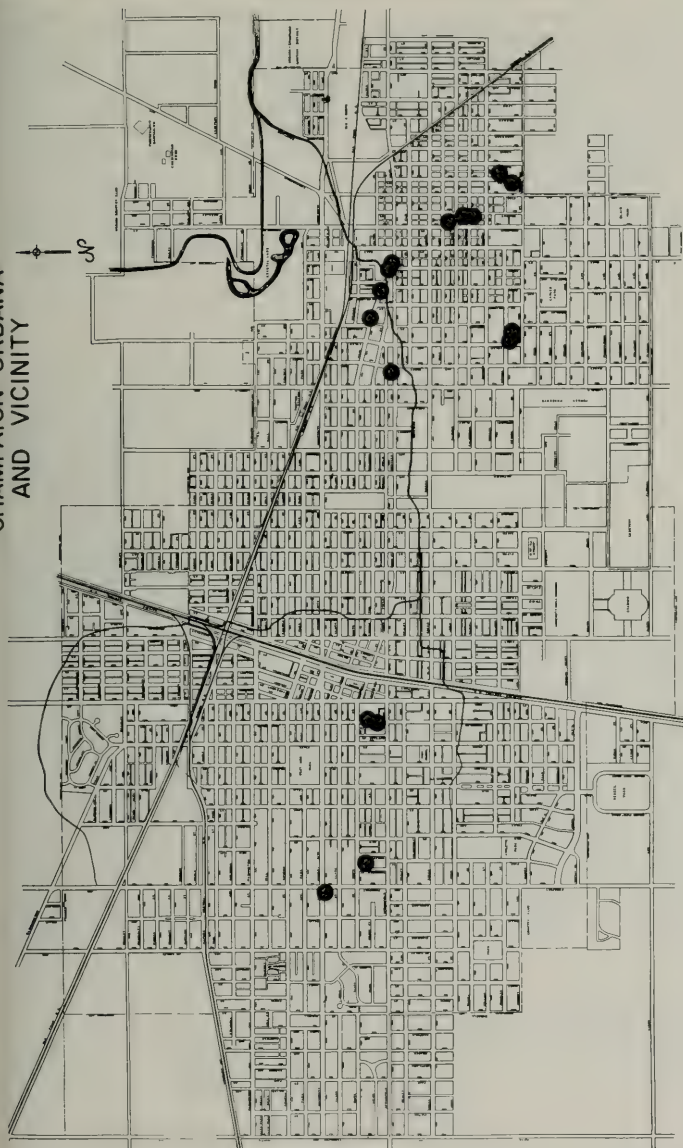
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Fig. 3.—Locations of 16 elms affected by phloem necrosis from 1944 through 1948 in Champaign-Urbana, Illinois.

Dutch elm disease, except seven elms removed in 1967 because of ice damage, were not included in the total number of trees recorded in this study. However, elms that became large enough to be seen from the street during the 29-year period were included.

The appearance and spread of each disease were recorded, starting with the first two trees attacked by phloem necrosis in 1944. Dutch elm disease did not appear until 1951.

Observations were made at irregular intervals during the growing season from 1944 through 1950 to determine the incidence and pattern of spread of phloem necrosis. Diseased trees were located by frequent scoutings. As many as 8-14 scoutings were made in a growing season.

After 1950, the authors made two surveys annually through 1972, one in June and one in September. However, in some years the first survey was not

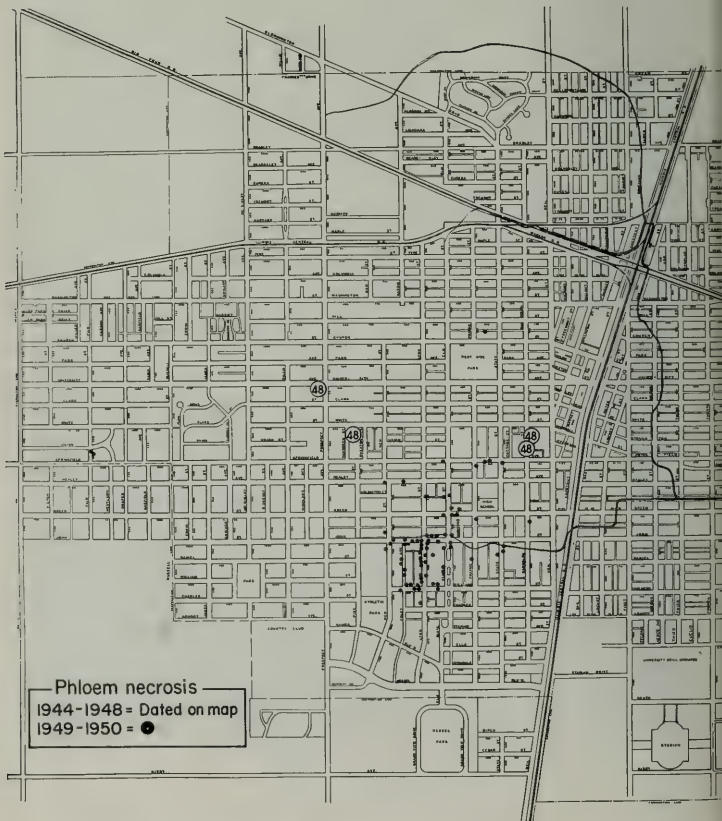


Fig. 4.—Distribution of 16 Champaign-Urbana, Illinois, elms affected by phloem necrosis from 1944 through 1948 (dated according to year when symptoms appeared) and of 412

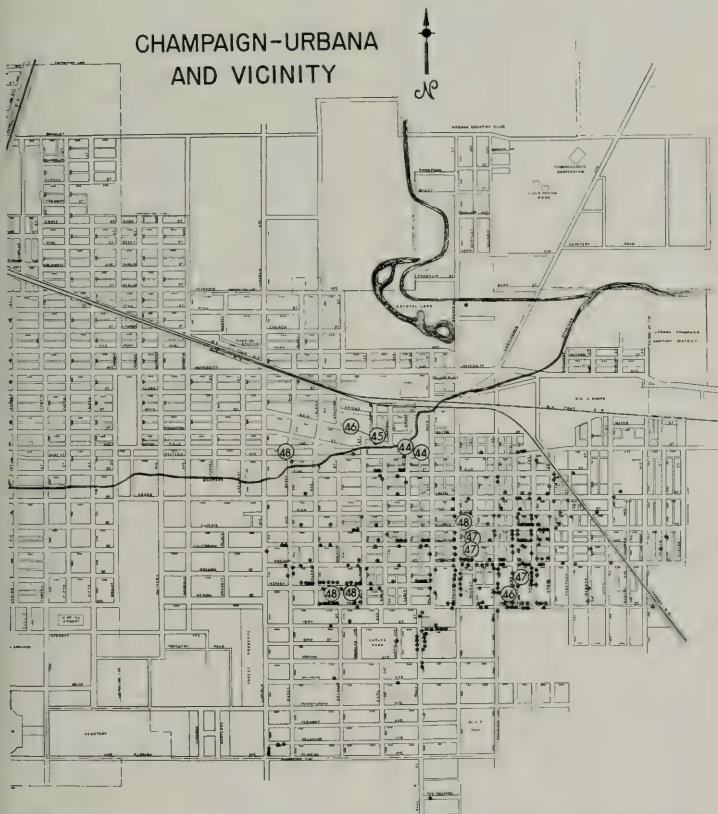
completed until early July and the second survey was not completed until early October. Each survey was made by observing all elms visible from the street while traveling by automobile. This type of survey necessitated driving 200 miles [320 km] of streets, which required a maximum driving time of 24 hours. We used our personal automobile, and the surveying was done in the evenings and on Saturdays.

The presence of phloem necrosis dur-

ing the years of low initial incidence, 1944-1948, was determined by examining the inner phloem for the butter-scotch color and wintergreen odor characteristic of the disease.

Dutch elm disease during the years of low initial incidence, 1951-1952, was identified by a laboratory culture test for the fungus.

Following the years of low initial incidence, each disease was recognized by foliage symptoms. Phloem necrosis-



elms affected by phloem necrosis in 1949 and 1950 (black dots). Some dots represent more than one tree where the elms were less than 30 feet [9 m] apart.

affected trees commonly show yellowing and wilting of leaves over the entire crown (Fig. 1), while Dutch elm disease-affected trees frequently have wilted foliage only on one or a few branches (Fig. 2). However, some Dutch elm disease-affected trees show general wilting on the entire crown. Leaves on such trees usually display less yellowing but more rapid browning and wilting than leaves show on phloem necrosis-affected trees. When there was doubt as to which disease was involved, a diagnosis was usually made by examining wood and bark samples. Also, the accuracy of diagnosis by observation from an automobile was tested by examining an occasional elm for wood and bark symptoms.

Data were recorded as to which disease was involved and whether a tree was wilting or dead. The stage or amount of wilt evident at the time of each survey was indicated by listing each tree showing the early, intermediate, or late stage of wilt. All dead elms were listed as dead, and all trees were listed by street address and whether on public or private property.

RESULTS

INITIAL SPREAD OF PHLOEM NECROSIS

Following the discovery in Urbana of phloem necrosis in two elms in 1944, one elm was affected by this disease in 1945, two in 1946, three in 1947, and eight in 1948 (Fig. 3). The tree affected in 1945 was about 300 feet [90 m] west of the two elms affected in 1944. Of the two elms affected in 1946, one was about 400 feet [120 m] farther west and one was about 1,900 feet [580 m] southeast of the elms affected in 1944 and 1945. Of the three elms affected in 1947, one was about 150 feet [45 m] northeast of a tree affected in 1946. The other two were on a line between trees affected in 1944 and 1946 and over 600 feet [180 m] from the nearest previously diseased elm. One of the eight elms affected

in 1948 was about 150 feet [45 m] north of an elm affected in 1947. The remaining seven elms were scattered west of previously affected trees. They ranged from about 700 to 8,000 feet [210–2,440 m] from the nearest previously diseased elms. Although the direction of the spread of phloem necrosis was generally west and south, each diseased tree was surrounded by numerous healthy elms.

The two elms that showed phloem necrosis symptoms in 1944 were in the 200 block of West Main Street in Urbana. They were among the oldest elms in the city. They were surrounded by numerous elms except for the three-square-block area of the business district of Urbana, starting in the 100 block of West Main Street. East of the business district, elms were abundant to the east city limit. Each of the 14 elms that became diseased from 1945 through 1948 represented a separate infection center, as none of them was within root-grafting distance of other affected trees (Himelick & Neely 1962; Verrall & Graham 1935). Each diseased tree was surrounded by healthy elms.

In 1949 and 1950 the number of diseased trees increased rapidly in Urbana. The disease was confined almost entirely to an area in south-central Urbana approximately 12 blocks square and extending south from the 200 block of West Main Street, the location of the two elms that first contracted phloem necrosis. By 1951, when Dutch elm disease was first found in Urbana, phloem necrosis was concentrated in this 12-block area and scattered at random in all directions around 7 of the 12 previously diseased Urbana elms, as shown in Fig. 4. The disease had not invaded an area six blocks wide along the west boundary of Urbana. In Champaign the disease appeared in the 700 block of South Lynn Street in 1949. By 1951 it had spread to many surrounding elms, as described subsequently. A few scattered elms north of this area and two elms within

two blocks of the west boundary of Champaign were also diseased. No elms were affected within the immediate areas surrounding the four Champaign elms that became diseased before 1949.

APPEARANCE AND SPREAD OF PHLOEM NECROSIS IN THE 700 BLOCK OF SOUTH LYNN STREET, CHAMPAIGN, 1949-1951

Only four elms showed symptoms of phloem necrosis in the entire city of Champaign in 1948, the year before the disease appeared in the 700 block of South Lynn Street. The nearest of these four elms was over 1,200 feet [370 m] northeast of the South Lynn Street 700 block (Fig. 4). Of the 36 elms in that block, 23 were on the west side of the street and 13 were on the east side. On the west side 21 were parkway trees and 2 were on private property, while 8 were parkway trees and 5 were on private property on the east side of the street. Each of the 21 parkway elms and 2 private-property elms on the west side of the street were within root-grafting distance of one or more elms (Fig. 5). The number of elms having phloem necrosis each year and the month in which symptoms were first observed are shown in Fig. 5.

On South Lynn Street, 8 elms wilted in 1949, 21 in 1950, and 7 in 1951. Of the eight elms that wilted in 1949, seven were on the west side of the street, and each was separated from the others by at least one elm that did not show wilt symptoms in 1949. Of 11 closely planted parkway elms on the west side of the street, every other one (5 trees) wilted in 1949, and the remaining 6 trees wilted in 1950.

The wilting of eight elms in 1949 suggests that the elm leafhopper, vector of the phloem necrosis MLO, fed extensively on the trees in this limited area before 1949. Since all 36 elms wilted within 3 years, all transmission of the MLO may have been by the elm leafhopper. However, most of the

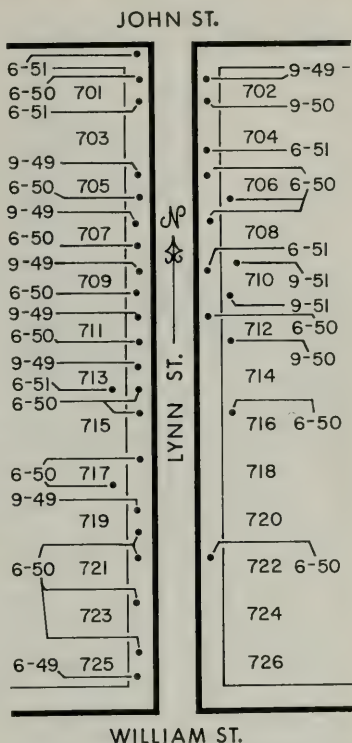


Fig. 5.—The spread of phloem necrosis, 1949-1951, in the 700 block of South Lynn Street, Champaign, Illinois.

elms that wilted in 1950 and 1951 were adjacent to elms that had wilted during the previous year, and they could have become infected through root-graft transmission of the MLO. Only three of the 36 elms were beyond root-grafting distance of other elms.

SPREAD OF PHLOEM NECROSIS IN 1951 AND 1952 AND INFLUENCE OF PHLOEM NECROSIS ON THE EARLY SPREAD OF DUTCH ELM DISEASE

The spread of phloem necrosis in Champaign-Urbana in 1951 and 1952 occurred among elms both within and

Table 2.—Spread of phloem necrosis in Champaign-Urbana, Illinois, in 1951 and 1952 in relation to the location of elms affected by phloem necrosis in the previous year.

Year	Diseased Elms	Elms Within Root-Grafting Distance of Previously Diseased Trees		Elms Beyond Root-Grafting Distance of Previously Diseased Trees	
		Number	Percent	Number	Percent
1951	359	116	32.3	243	67.7
1952	555	186	33.5	369	66.5
<i>Total or percent</i>	<i>914</i>	<i>302</i>	<i>33.0</i>	<i>612</i>	<i>67.0</i>

beyond root-grafting distance of previously affected trees. Of the 914 elms affected by phloem necrosis in 1951 and 1952, 33 percent were within and 67 percent were beyond root-grafting distance of previously affected trees (Table 2). The affected elms that were beyond root-grafting distance of previously affected elms were widely and randomly scattered at distances of 50 feet [15 m] to more than 1,000 feet [300 m] from previously diseased trees.

With the appearance of Dutch elm disease in a single elm in the 800 block of West Pennsylvania Avenue in southwest Urbana in 1951, our data on the incidence of phloem necrosis were examined to determine the influence of phloem necrosis on the appearance and early spread of Dutch elm disease. The relationship of phloem necrosis to the appearance and early spread of Dutch elm disease is indicated by the fact that phloem necrosis-affected elms can harbor both the smaller European elm bark beetle and the Dutch elm disease fungus. Data originally gathered in Urbana by E. B. Himelick in 1952 showed that 8 of 40 elms dying from phloem necrosis were infested with the bark beetles and the fungus (Campana 1954:358). Apparently the Dutch elm disease fungus had been introduced into the phloem necrosis-affected elms by the bark beetles.

The population of the smaller European elm bark beetle is largely determined by the amount of elm material available for colonization. Since there was no community-wide program for the control of either disease in Champaign-Urbana, most of the diseased

trees were left standing for several weeks, months, or a year or more after they had died. These trees served as abundant colonizing locations for the bark beetles. The number of standing dead elms in June and September in 1951, 1952, and 1953 (Table 3) was greater than the number of elms wilting from phloem necrosis in these same months except in June 1951. Under these conditions millions of the smaller European elm bark beetles were present in the area and were potential carriers of the Dutch elm disease fungus.

Table 3.—Number of phloem necrosis-affected elms, wilting and dead, standing in Champaign-Urbana, Illinois, in June and September 1951, 1952, and 1953.

Year	Elms Dead from Phloem Necrosis		Elms Wilting from Phloem Necrosis	
	June	September	June	September
1951	213	187	218	141
1952	324	558	239	316
1953	589	441	193	195
<i>Total</i>	<i>1,126</i>	<i>1,186</i>	<i>650</i>	<i>652</i>

APPEARANCE OF DUTCH ELM DISEASE AND LOCATIONS OF ELMs HAVING DUTCH ELM DISEASE, 1951-1953

Dutch elm disease first appeared in the Champaign-Urbana area in 1951 when a single affected elm was found in the 800 block of West Pennsylvania Avenue in southwest Urbana. We verified the disease by culturing the fungus from samples of the brown, discolored sapwood of wilted branches. Phloem necrosis also spread to this immediate area in 1951 when two elms showed symptoms of that disease.

Eleven elms were killed by Dutch elm disease in the Champaign-Urbana area in 1952. Of these 11 elms, 3 were adjacent to elms that were wilting

CHAMPAIGN-URBANA AND VICINITY

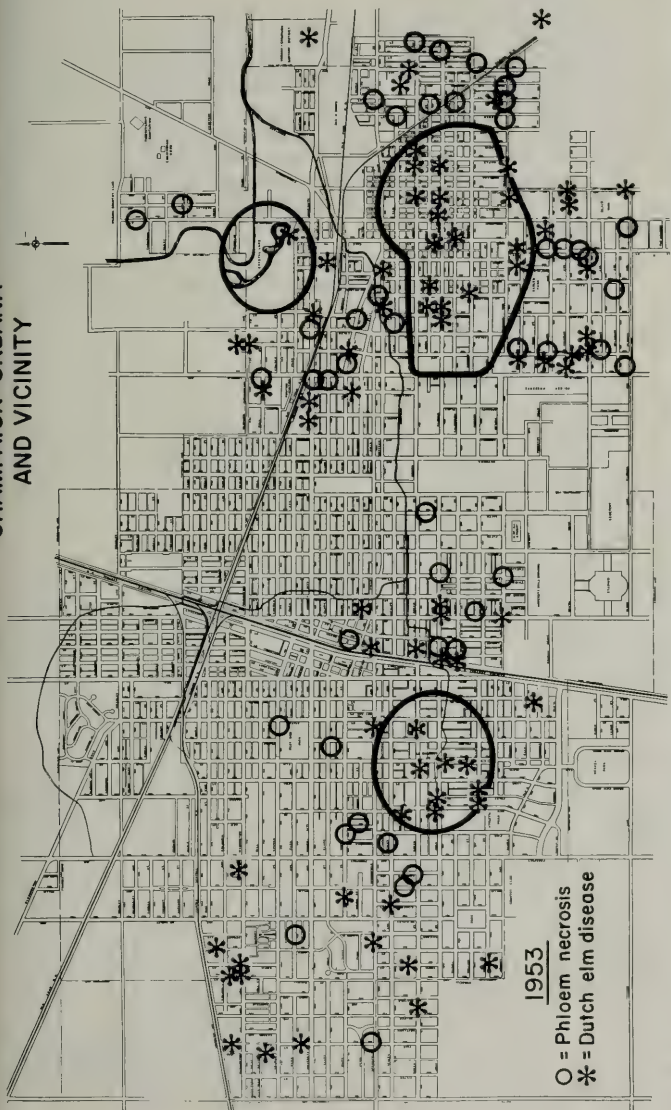


Fig. 6.—Distribution of elms affected by phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, in 1953. The three areas enclosed by heavy lines show locations of Dutch elm disease-affected elms in areas where phloem necrosis was abundant.

from or had been killed by phloem necrosis. Of these three, one was adjacent to a phloem necrosis-affected elm that wilted in 1950 and 1951 and was dead by 1952. One was adjacent to an elm that wilted in 1950, and one was adjacent to two elms. One of these two elms wilted in 1950, and the other wilted in 1951. The remaining eight elms affected by Dutch elm disease in 1952 were isolated trees that were not adjacent to phloem necrosis-affected elms or to the one elm affected by Dutch elm disease in 1951.

The locations of 164 elms affected by Dutch elm disease in 1953 and their relation to phloem necrosis-affected elms are shown in Fig. 6 (some locations represent more than one tree). Twenty-seven locations of Dutch elm disease-affected elms were in areas where phloem necrosis was abundant, as indicated by the three areas enclosed by heavy lines in Fig. 6. Ten other locations were immediately adjacent to one or more phloem necrosis-affected elms. The locations of the remaining 41 Dutch elm disease-affected trees

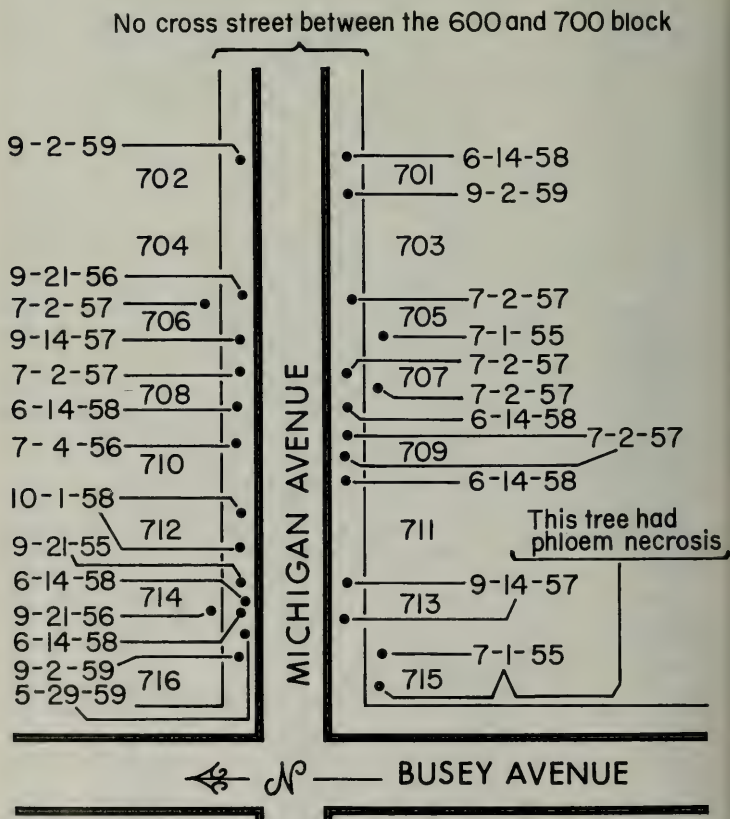


Fig. 7.—The spread of Dutch elm disease, 1955–1959, in the 700 block of West Michigan Avenue, Urbana, Illinois.

were not adjacent to phloem necrosis-affected elms but were widely scattered throughout much of the Champaign-Urbana area.

Only one of the 176 elms affected by Dutch elm disease during this 3-year period, 1951-1953, was within root-grafting distance of an elm previously affected by Dutch elm disease. This one elm wilted in 1953 and was adjacent to an elm that wilted in 1952. Therefore, the Dutch elm disease fungus was carried to the remaining 175 elms by elm bark beetles.

SPREAD OF DUTCH ELM DISEASE IN THE 700 BLOCK OF WEST MICHIGAN AVENUE, URBANA, 1955-1959

Elms began dying in the 700 block of West Michigan Avenue, Urbana, in 1955, when four elms wilted, three from Dutch elm disease and one from phloem necrosis. Elms affected by Dutch elm disease before 1955 within one block of this area were: one in 1951, two in 1953, and three in 1954. Phloem necrosis did not occur within one block of this area before 1955.

There were 29 American elms (23 in the parkway and 6 on private property) in this area in June 1955 when the first 3 showed wilt symptoms of Dutch elm disease. The location of each tree is indicated in Fig. 7. The date is shown when wilt symptoms were first observed on each tree. The annual loss of elms is given in Table 4.

Of the 28 elms killed in this block by Dutch elm disease in 5 years, more (10 trees) were killed in the third year than in any other year of the study. No elm within root-grafting distance of previously diseased trees showed wilt symptoms in the second year. Thirteen (46 percent) of the trees were within root-grafting distance of previously diseased trees. Therefore, they may have become infected through roots grafted to those of previously diseased elms. The remaining 15 elms (54 percent), not within root-grafting distance of previously diseased trees, became infected

Table 4.—Elms killed annually by Dutch elm disease in the 700 block of West Michigan Avenue, Urbana, Illinois, 1955-1959.

Year	Residual Population	Elms Killed by Dutch Elm Disease			Elms Within Root-Grafting Distance of Previously Diseased Trees			Elms Beyond Root-Grafting Distance of Previously Diseased Trees		
		Number	Percent		Number	Percent		Number	Percent	
			Original Population	Residual Population		Original Population	Residual Population		Original Population	Residual Population
1955	28 ^a	3	11	11	..	..	..	3	11	11
1956	25	3	11	12	..	..	..	3	11	12
1957	22	10	36	45	5	18	23	5	18	23
1958	12	8	28	67	6	21	50	2	7	17
1959	4	4	14	100	2	7	50	2	7	50
Total or percent		28	100		13	46		15	54	

^a One elm died from phloem necrosis in 1955 and is not included in this table.

through insect transmission of the fungus.

SPREAD OF PHLOEM NECROSIS AND DUTCH ELM DISEASE ON SPRINGFIELD AVENUE, CHAMPAIGN, 1955-1959

Elms in a six-block section of East Springfield Avenue, Champaign, between First and Wright Streets, began dying in 1955 when one elm wilted from Dutch elm disease. Phloem necrosis did not appear in this area until 1957, when one elm contracted that disease. Several elms within three blocks of Springfield Avenue were attacked by each of these diseases before 1955. Two elms died from phloem necrosis in 1953, one located two blocks northwest of the

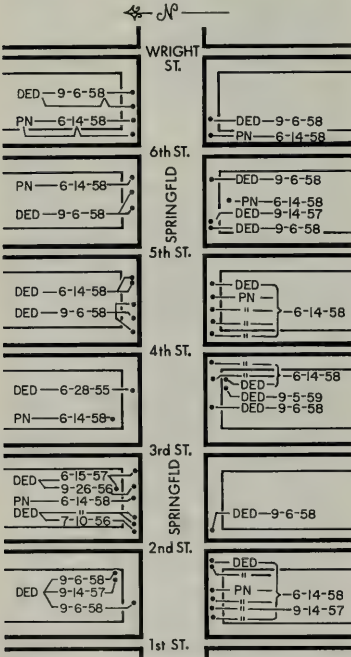


Fig. 8.—The spread of phloem necrosis (PN) and Dutch elm disease (DED) on East Springfield Avenue, Champaign, Illinois, 1955-1959.

Table 5.—Elms killed annually by phloem necrosis and Dutch elm disease in the 100-600 blocks of East Springfield Avenue, Champaign, Illinois, 1955-1959.

Year	Residual Elm Population	Elms Killed by Phloem Necrosis			Elms Killed by Dutch Elm Disease			Elms Killed by Both Diseases		
		Number	Percent		Number	Percent		Number	Percent	
			Original Population	Residual Population					Original Population	Residual Population
1955	47	..	..	..	1	2	2	1	2	2
1956	46	..	..	..	2	4	4	2	4	4
1957	44	1	2	2	4	9	9	5	11	11
1958	39	16	34	41	22	47	56	38	81	97
1959	1	..	..	..	1	2	100	1	2	100
Total or percent		17	36		30	64		47	100	

100 block and one located two and one-half blocks south of the 600 block of East Springfield Avenue. Twelve elms died from Dutch elm disease, two in 1953 and ten in 1954. One of the two elms that died in 1953 was two blocks west and one was one block north of the 100 block of East Springfield Avenue. Of the 10 elms that died in 1954, 7 were one block distant from the 100 and 200 blocks, and 3 were two blocks from the 400 block of East Springfield Avenue.

The parkway along this six-block stretch was lined with 40 Moline elms in 1950. Each tree was approximately 1 foot [0.3 m] in trunk diameter. Seven larger American elms along the same section were located on private property. The locations of these 47 elms are indicated in Fig. 8. The 25 elms that wilted in 1955 on streets that cross East Springfield Avenue were beyond root-grafting distance of the elms along Springfield Avenue. All 47 elms on

East Springfield Avenue became affected by phloem necrosis or Dutch elm disease and died within 5 years, 1955-1959.

Of the 47 elms killed in 5 years along East Springfield Avenue, Champaign, 17 (36 percent) were killed in 2 years by phloem necrosis, while 30 (64 percent) were killed in 5 years by Dutch elm disease. The disease involved and the year that each tree became diseased are shown in Table 5.

A rapid increase in the number of trees affected by each disease occurred in the year following the appearance of phloem necrosis and in the third year following the appearance of Dutch elm disease. Two of the trees killed by phloem necrosis on the south side of the 100 block of East Springfield Avenue in 1958 were within root-grafting distance of a tree killed by phloem necrosis in 1957 (Fig. 9). Six of the trees on East Springfield Avenue killed by Dutch elm disease between 1955 and



Fig. 9.—Moline elms on the south side of the 100 block of East Springfield Avenue, Champaign, Illinois. The first four elms on the right were killed by phloem necrosis. The fifth elm and one elm east of this fifth tree, removed before the picture was taken, were killed by Dutch elm disease. The second elm from the right died in 1957, and the others died in 1958. (Photo by W. E. Clark)

1959 were within root-grafting distance of trees killed by Dutch elm disease in the previous 1 or 2 years. Three of these six elms were on the north side of the 200 block, one on the north side of the 100 block, one on the south side of the 300 block, and one on the south side of the 500 block.

Since 39 of the 47 elms in this area were not within root-grafting distance of previously diseased trees, the spread of each disease occurred mainly by insect transmission of each causal agent.

PHLOEM NECROSIS-AFFECTED ELMS THAT LATER SHOWED SYMPTOMS OF DUTCH ELM DISEASE

Some elms affected by phloem necrosis subsequently became affected by Dutch elm disease before dying. The number of elms that showed phloem necrosis symptoms followed by Dutch elm disease symptoms from 1954 to 1960 is listed in Table 6. During this 7-year period 1,234 trees were affected by phloem necrosis and 10,714 trees were affected by Dutch elm disease. The data are arranged according to the time between the first appearance of phloem necrosis symptoms and the subsequent appearance of Dutch elm disease symptoms.

Of the 153 elms affected by both diseases, 28 (18.3 percent) were affected by Dutch elm disease in Sep-

tember following the appearance of phloem necrosis symptoms in the previous June, 123 (80.4 percent) in the year following the appearance of phloem necrosis symptoms, and only two (1.3 percent) in the second year following the appearance of phloem necrosis symptoms. In general, the percentage of phloem necrosis-affected elms that subsequently showed Dutch elm disease increased as the number of elms affected by Dutch elm disease increased. Many elms that become infected with the Dutch elm disease fungus in June wilt during the same growing season. Therefore, it is not surprising that 28 elms that showed phloem necrosis symptoms in June showed Dutch elm disease symptoms by the following September. Elms which had been wilting from phloem necrosis in June and were wilting from Dutch elm disease in September most likely became infected by the Dutch elm disease fungus in June, when phloem necrosis symptoms were already evident.

INCIDENCE OF PHLOEM NECROSIS AND DUTCH ELM DISEASE IN CHAMPAIGN-URBANA, 1944-1972

To determine the incidence of phloem necrosis and Dutch elm disease in Champaign-Urbana, the number of elms affected annually by each disease

Table 6.—Phloem necrosis-affected elms in Champaign-Urbana, Illinois, that subsequently contracted Dutch elm disease, 1954-1960.

Year	Elms Affected by Phloem Necrosis	Elms Showing Dutch Elm Disease Symptoms			Phloem Necrosis-Affected Elms That Later Showed Dutch Elm Disease Symptoms	
		Same Year*	1 Year Later	2 Years Later	Number	Percent
1954	179	..	13	..	13	7.3
1955	123	..	..	..	..	
1956	60	1	5	..	6	10.0
1957	368	1	42	2	45	12.2
1958	344	25	45	..	70	20.3
1959	148	..	17	..	17	11.5
1960	12	1	1	..	2	16.7
Total or percent	1,234	28	123	2	153	12.4

* Trees listed in this column showed phloem necrosis symptoms in the June survey and Dutch elm disease symptoms in the following September survey.

Table 7.—Elms killed by phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, from 1944 through 1972.

Year	Residual Elm Population	Elms Killed Annually by Phloem Necrosis			Elms Killed Annually by Dutch Elm Disease			Elms Killed Annually by Both Diseases		
		Number	Percent of Original Population	Percent of Residual Population	Number	Percent of Original Population	Percent of Residual Population	Number	Percent of Original Population ^a	Percent of Residual Population ^a
1944	14,103	2	0.01	0.01	...	...	...	2	0.01	0.01
1945	14,101	1	0.01	0.01	...	...	...	1	0.01	0.01
1946	14,100	2	0.01	0.01	...	...	...	2	0.01	0.01
1947	14,098	3	0.02	0.02	...	...	...	3	0.02	0.02
1948	14,095	8	0.06	0.06	...	...	...	8	0.06	0.06
1949	14,087	99	0.70	0.70	...	...	...	99	0.70	0.70
1950	13,988	313	2.22	2.24	...	...	...	313	2.22	2.24
1951	13,675	359	2.55	2.63	1	0.01	0.01	360	2.55	2.63
1952	13,315	555	3.94	4.17	11	0.08	0.08	566	4.01	4.25
1953	12,749	388	2.75	3.04	164	1.16	1.29	552	3.91	4.33
1954	12,197	179	1.27	1.47	694	4.92	5.69	873	6.19	7.16
1955	11,324	123	0.87	1.09	1,805	12.80	15.94	1,928	13.67	17.03
1956	9,396	60	0.43	0.64	1,836	13.02	19.54	1,896	13.44	20.18
1957	7,500	368	2.61	4.91	2,116	15.00	28.21	2,484	17.61	33.12
1958	5,016	344	2.44	6.86	1,770	12.55	35.29	2,114	14.99	42.15
1959	2,902	148	1.05	5.10	1,804	12.79	62.16	1,952	13.84	67.26
1960	950	12	0.09	1.26	689	4.89	72.53	701	4.97	73.79
1961	249	3	0.02	1.20	119	0.84	47.79	122	0.86	49.00
1962	127	1	0.01	0.79	31	0.22	24.41	32	0.23	25.20
1963	95	4	0.03	4.21	9	0.06	9.47	13	0.09	13.68
1964	82	4	0.03	4.88	1	0.01	1.22	5	0.04	6.10
1965	77	1	0.01	1.30	4	0.03	5.19	5	0.04	6.49
1966	72	1	0.01	1.39	1	0.01	1.39	2	0.01	2.78
1967	70	3	0.02	4.29	0	...	...	3	0.02	4.29
1968	60 ^b	2	0.01	3.33	1	0.01	1.67	3	0.02	5.00
1969	57	0	...	...	1	0.01	1.75	1	0.01	1.75
1970	56	3	0.02	5.36	0	...	...	3	0.02	5.36
1971	53	5	0.04	9.43	0	...	...	5	0.04	9.43
1972	48	3	0.02	6.25	5	0.04	10.42	8	0.06	16.67
Total or percent		2,994	21.23		11,062	78.44		14,056	99.67	

^a Some percentages in this column are not exact totals of the corresponding percentages in preceding columns because all percentages have been rounded to two decimal places.

^b Seven trees that were not diseased but were severely damaged by ice in January 1968 were removed. Healthy trees removed because of construction or any other cause have not been included in this study.

was recorded from 1944, when phloem necrosis first appeared, through 1972. The number of elms affected annually and the percentages of the original and residual elm populations lost each year are recorded in Table 7. The percentages of the original elm population lost annually to each disease are illustrated in Fig. 10. The percentages of the residual elm population lost annually to each disease are illustrated in Fig. 11.

Phloem Necrosis

A rapid increase in the number of elms affected by phloem necrosis did not occur until 1949, 5 years after the disease had first appeared in two Urbana elms. The number of elms affected by phloem necrosis in Champaign-Urbana increased annually until 1952, when 555 were affected. Following 1952 the number of phloem necrosis-diseased trees decreased annually until 1956, when only 60 elms were killed. This decrease was followed by an increase to 368 affected trees in 1957. After 1957 the number of phloem necrosis-diseased trees decreased rapidly until 1960, when only 12 elms were

affected. From 1961 through 1972 only one to five elms were affected by phloem necrosis annually except in 1969, when no phloem necrosis occurred. From 1944 through 1972, a period of 29 years, 2,994 elms were killed by phloem necrosis.

The two peak periods of elm deaths from phloem necrosis occurred in 1952 and 1957 (Fig. 10). The cause for the high death rate of elms in 1952 and the subsequent decrease in the incidence of phloem necrosis through 1956 was not determined. However, four conditions that may have been involved were (1) the rapid increase in the incidence of Dutch elm disease, (2) the reduction in the elm population, (3) the time required for symptoms of phloem necrosis to appear following infection, and (4) drought conditions from 1952 through 1955.

The incidence of Dutch elm disease increased from 11 trees in 1952 to 1,805 trees in 1955. During this period Dutch elm disease reduced the elm population by 2,674 trees, or 20 percent of the elm population of 1952.

The time required for wilt symptoms to appear following infection is longer

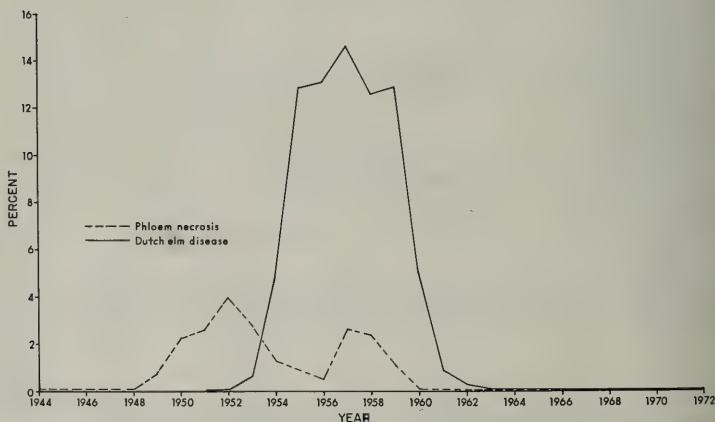


Fig. 10.—Annual percentages of the original population of 14,103 elms lost to phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, 1944–1972.

for phloem necrosis than for Dutch elm disease. Phloem necrosis-affected elms do not show foliage symptoms for at least 1 year following infection, while many Dutch elm disease-affected elms show foliage symptoms in the year when infection occurs.

Drought conditions that prevailed from 1952 through 1955, especially in 1953 and 1954, may have caused a reduction in the elm leafhopper population, since this insect is adversely affected by such conditions. Precipitation for the 5-month growing season, May through September, was 7.89 inches [200.41 mm] below normal in 1953 and 4.19 inches [106.41 mm] below normal in 1954. Total precipitation was 10.34 inches [262.64 mm] below normal in 1953 and 6.73 inches [170.94 mm] below normal in 1954 (Carter 1955:40). Collection records of the Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, show that the populations of leafhoppers in general were drastically reduced during these drought years and that the elm leafhopper has never been collected in abundance in Illinois.

The increase in the incidence of

phloem necrosis from 1957 through 1959 may have been influenced mainly by an increase in the elm leafhopper population, which might be expected in years of near-normal rainfall. Following 1959 the incidence of phloem necrosis decreased to very low levels during the period of rapid decline in the residual elm population. Only 7 percent of the original elm population remained by 1960.

Dutch Elm Disease

A rapid increase in the number of elms affected by Dutch elm disease started in 1953, 2 years after the disease first appeared in Urbana in a single elm. The number of elms affected annually by Dutch elm disease increased until 1957, when 2,116 trees were affected. During the 5-year period 1955–1959, the annual loss of elms to Dutch elm disease was 1,770–2,116, with a total loss of 9,331 trees. This number was 82.4 percent of the residual elm population of 11,324 trees in the spring of 1955, or 66.2 percent of the original elm population of 14,103 trees in 1944.

The peak incidence of Dutch elm disease (Fig. 10) occurred in 1957, 6

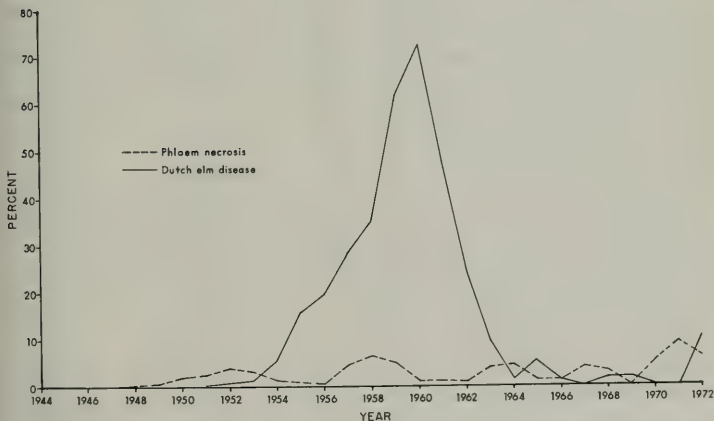


Fig. 11.—Annual percentages of the residual population of elms lost to phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, 1944–1972.

years after the disease first appeared in the area. The number of elms killed in 1957 was 2,116, or 15 percent of the original elm population and 28.21 percent of the residual elm population. Following 1959 the residual elm population decreased rapidly until 1963, when only 95 healthy elms remained and only 9 were killed by Dutch elm disease. With the rapid decline in the elm population, the incidence of Dutch elm disease also declined drastically. From 1964 to 1969 only one to four trees (none in 1967) became affected by this disease annually. No elms were affected in 1970 and 1971, but five elms were affected in 1972.

Figure 10 shows that the incidence of Dutch elm disease increased more rapidly, reached a much higher peak, and decreased more rapidly than did the incidence of phloem necrosis. Additionally, only one peak period of elm deaths from Dutch elm disease occurred, while there were two peak periods of elm deaths from phloem necrosis.

Effect of Each Disease on the Residual Population of Elms

The annual loss of elms from each disease in relation to the residual elm population is illustrated in Fig. 11. The annual loss from phloem necrosis fluctuated from year to year, reaching five peaks of 5 percent or more of the residual elm population. The highest peak (9.43 percent) occurred in 1971, when the residual elm population was only 53 trees. The next highest peak occurred in 1958, when the residual elm population was 5,016 trees.

Following the appearance of Dutch elm disease in 1951, the percentage of the residual elm population killed annually by this disease increased rapidly until 1960. In 1960 Dutch elm disease killed 689 trees (72.53 percent) of the residual elm population of 950 trees. Following 1960 the annual loss of trees in the residual elm population decreased rapidly until 1964 when only

1 elm (1.22 percent) of the residual population of 82 was killed by Dutch elm disease.

Accumulated Percentages of Elms Killed by Each Disease, 1944-1972

The accumulated percentages of elms killed by each disease are given in Table 8 and illustrated in Fig. 12. The loss of elms from each disease follows a sigmoid curve. Less than 10 percent of the elm population was killed by both diseases from 1944 through 1952, a period of 9 years. Phloem necrosis was present throughout the 9-year period, but Dutch elm disease was present for only 2 years. During the second 9-year period, 1953-1961, both diseases killed more than 89 percent of the

Table 8.—Accumulated percentages of elms killed by phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, from 1944 through 1972.

Year	Percent of Elms Killed by	
	Phloem Necrosis	Dutch Elm Disease
1944	0.01	...
1945	0.02	...
1946	0.04	...
1947	0.06	...
1948	0.11	...
1949	0.32	...
1950	3.03	...
1951	5.58	0.01
1952	9.52	0.09
1953	12.27	1.25
1954	13.54	6.17
1955	14.41	18.97
1956	14.83	31.99
1957	17.44	46.99
1958	19.88	59.54
1959	20.93	72.33
1960	21.02	77.22
1961	21.04	78.06
1962	21.05	78.28
1963	21.07	78.34
1964	21.10	78.35
1965	21.11	78.38
1966	21.12	78.39
1967	21.14	78.39
1968	21.15	78.39
1969	21.15	78.40
1970	21.17	78.40
1971	21.21	78.40
1972	21.23	78.44

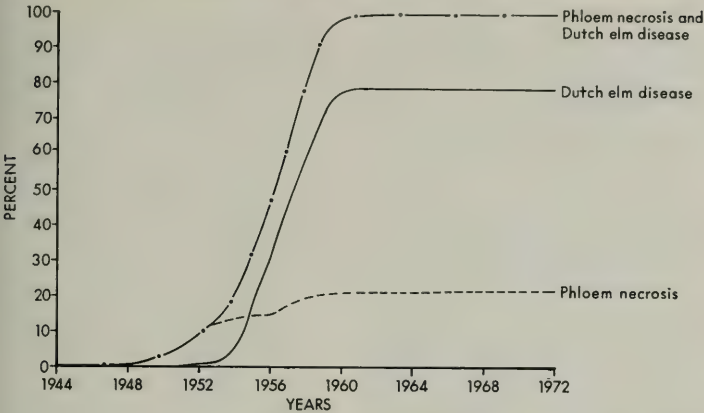


Fig. 12.—Accumulated percentages of the original population of 14,103 elms lost each year to phloem necrosis and Dutch elm disease in Champaign-Urbana, Illinois, 1944–1972.

original elm population. With less than 1 percent of the elms remaining after 18 years, the annual loss became a few trees. Phloem necrosis killed 2,994 elms during the 29-year period, 1944–1972, while Dutch elm disease killed 11,062 elms during the 22-year period, 1951–1972. Although no elms showed symptoms of Dutch elm disease in 1970 or 1971, five trees were killed by the disease in 1972. Of the original population of 14,103 elms in 1944, all but 40 had been killed by the fall of 1972, a period of 29 years.

TIME OF YEAR IN WHICH ELMS DIED FROM PHLOEM NECROSIS AND DUTCH ELM DISEASE

Starting in 1951 two surveys were made annually to record the number of elms affected by phloem necrosis and by Dutch elm disease. The first survey was made in the early part of the growing season, usually in June. The second survey was made in the late part of the growing season, usually in September. These surveys are referred to as the June and September surveys. Each year data were obtained on the

Table 9.—Elms showing disease symptoms in June and September surveys, Champaign-Urbana, Illinois, 1955–1961.

Year	Elms Having Phloem Necrosis Symptoms			Elms Having Dutch Elm Disease Symptoms			Total Diseased Elms	Standing Dead Elms	
	June Survey	September Survey	Total	June Survey	September Survey	Total		June Survey	September Survey
1955	40	81	121	1,059	746	1,805	1,926	86	133
1956	21	39	60	1,162	674	1,836	1,896	160	528
1957	44	324	368	1,159	957	2,116	2,484	255	520
1958	217	127	344	1,049	721	1,770	2,114	447	1,323
1959	58	90	148	1,116	688	1,804	1,952	1,064	1,509
1960	4	8	12	496	193	689	701	608	341
1961	2	1	3	92	27	119	122	...	...
Total	386	670	1,056	6,133	4,006	10,139	11,195	2,620	4,354

number of elms affected by each disease in each of the two survey periods. No affected elm was included in the data of more than one survey. The numbers of elms affected by each disease at the time of each June and September survey from 1955 through 1961 are recorded in Table 9.

Of the 1,056 elms affected by phloem necrosis during this 7-year period, 386 (36.6 percent) showed symptoms in June, and 670 (63.4 percent) showed symptoms in September. Of the 10,139 elms affected by Dutch elm disease, 6,133 (60.5 percent) showed symptoms in June, and 4,006 (39.5 percent) showed symptoms in September. Of the 6,974 dead elms standing at the time of the June and the September surveys during the years 1955-1960, 2,620 (37.6 percent) were standing in June and 4,354 (62.4 percent) were standing in September.

PERIOD OF TIME IN WHICH ELMS DIED FOLLOWING THE APPEARANCE OF FOLIAGE WILT OF PHLOEM NECROSIS OR DUTCH ELM DISEASE

Not all elms affected by phloem necrosis or Dutch elm disease die in the same growing season in which foliage wilt first appears. Some elms wilt during two, and occasionally three, growing seasons before they die; some elms that have shown no foliage wilt die during the winter. Data on 231 elms affected by phloem necrosis, 3,908 elms affected by Dutch elm disease, and 820 elms that died but showed no foliage wilt are given in Table 10. The data cover the growing seasons of 1955 through 1960. During this period most diseased elms were not removed until after they were dead. This practice made it possible to record the period of time in which the diseased trees died.

Of the 231 phloem necrosis-affected elms, 143 (61.9 percent) died in the year following the appearance of wilt. Only 87 (37.7 percent) died in the year that wilt appeared, and only 1 (0.4 percent) lived until the second year fol-

Table 10.—The period of time in which elms died following the appearance of wilt symptoms of phloem necrosis or Dutch elm disease, Champaign-Urbana, Illinois, 1955-1960.

Year	Elms Showing Phloem Necrosis Wilt That Died					Elms Showing Dutch Elm Disease Wilt That Died					Elms That Died in Winter Without Showing Wilt	
	Same Year		1 Year Later		2 Years Later	Same Year		1 Year Later		2 Years Later	June	September
	Wilted in June	Not Wilted in June	Wilted in June	Not Wilted in June		Wilted in June	Not Wilted in June	Wilted in June	Not Wilted in June			
1955	13	2	..	..	..	247	119	..	..	..	..	79
1956	..	..	3	..	..	94	102	37	9	..	..	66
1957	..	17	10	..	..	235	227	39	19	3	2	89
1958	11	21	47	19	..	426	736	80	84	2	1	169
1959	14	9	30	17	1	462	302	205	107	9	1	273
1960	..	..	16	1	..	101	83	137	36	3	..	144
Total	38	49	106	37	1	1,565	1,569	498	255	17	4	820

lowing the appearance of wilt. Nearly half (45.9 percent) of the elms affected by phloem necrosis continued to live during the remainder of the summer in which wilt symptoms appeared but were dead by June of the next summer.

Of the 3,908 Dutch elm disease-affected elms, 3,134 (80.2 percent) died in the year when wilt symptoms appeared. Only 753 (19.3 percent) died during the second year, and 21 (0.5 percent) died during the third summer. These data indicate that, following the initial appearance of foliage wilt, elms having Dutch elm disease die more rapidly than do elms affected by phloem necrosis.

Also of interest are the 820 elms that did not show foliage wilt in the September survey but died before the June survey of the following year. These elms represent 16.5 percent of the 4,959 elms that died during the 6-year period. Although the cause of death was not determined, probably most, if not all, of these elms were killed by Dutch elm disease, since this disease usually causes elms to die more rapidly than does phloem necrosis.

DISCUSSION

Phloem necrosis was not known to occur in any areas close to Champaign-Urbana when the disease was discovered in two adjacent elms in Urbana in 1944. The nearest area where the disease had occurred was Danville, Illinois, 32 miles [51 km] east of Urbana. Beginning in 1935, elm plantings between Urbana and Danville had been observed for disease symptoms frequently during the growing season of each year.

In the course of this study careful examination of phloem samples from wilting elms showed that the characteristic butterscotch color usually was present only in the current phloem. However, samples from some wilting elms had butterscotch color in 1- and sometimes 2-year-old phloem. This condition occurred mainly in elms that

showed foliage symptoms during two or more growing seasons. Since the butterscotch color in the current phloem indicates that the tree has been infected for about 1 year (Baker 1949:730), the butterscotch color in 1- and 2-year-old phloem indicates that the MLO is in some elms for 2-3 years before foliage wilt appears.

Because phloem necrosis was present in the Champaign-Urbana area 7 years (1944-1950) before Dutch elm disease appeared there, the initial spread of phloem necrosis was not influenced by Dutch elm disease. In Urbana, phloem necrosis spread slowly for 4 years following its appearance in 1944. The few affected trees were widely scattered at distances of approximately 300-2,000 feet [100-600 m] from the two elms first attacked. Each affected tree represented a new center of infection from which the disease continued to spread to nearby elms. This initial spread resulted from transmission of the MLO by the elm leafhopper.

The incidence of phloem necrosis increased rapidly in Urbana during 1948 and 1949, and by 1950 over 300 trees were affected. The disease was concentrated mainly within an area approximately 1,400 feet [400 m] wide and 4,000 feet [1,200 m] long in the central part of the city, an area heavily populated with American elms. By 1950 only a few scattered elms were affected beyond this area, and no affected trees were in the 3,600-foot-wide [1,100 m] area adjacent to Champaign.

In Champaign phloem necrosis was not found until 1948, when it affected four elms. The trees were approximately 5,000 feet [1,500 m] west of any affected trees in Urbana. Following 1948 the number of elms affected by phloem necrosis increased rapidly in Champaign, and all but a few of the affected trees were concentrated in an area two blocks wide and four blocks long, centering around the 700 block of South Lynn Street.

Of the 36 elms in the 700 block of South Lynn Street, 8 wilted in 1949.

The infection of these eight elms resulted from insect transmission of the MLO in 1948 or earlier. Because 28 of the elms in this block wilted in the 2 years following the initial appearance of the disease, it is possible that the MLO was spread by the elm leafhopper. However, all but three of these elms were within root-grafting distance of previously affected trees. Following 1950 phloem necrosis spread rapidly throughout both cities, and the greatest loss of trees from this disease in any 1 year occurred in 1952, 8 years after the disease first appeared.

Phloem necrosis was widespread when Dutch elm disease was discovered in one elm in southwest Urbana in 1951. The infection of this elm resulted from insect transmission of the fungus. However, phloem necrosis-affected elms may have harbored the inoculum, because the Dutch elm disease fungus was isolated from 8 of 40 elms that had phloem necrosis in 1952 (Campana 1954:358). Therefore, many of the hundreds of elms killed annually by phloem necrosis but not removed promptly served as colonizing sites for the smaller European elm bark beetle, vector of the Dutch elm disease fungus. Millions of these insects were present in the Champaign-Urbana area as potential carriers of the Dutch elm disease fungus at the time the disease first appeared.

Following the appearance of Dutch elm disease in 1951, the fungus was transmitted by insects in 1952 and 1953, for only 1 of 175 diseased elms was within root-grafting distance of a previously diseased tree. Although only a few elms were affected in 1952, Dutch elm disease spread rapidly in the next 3 years, and a 5-year peak period of elm deaths started in 1955. Dutch elm disease increased annually more rapidly than did phloem necrosis in the number of elms affected and in the number of infection centers. As the incidence of Dutch elm disease increased, the incidence of phloem necrosis decreased,

and phloem necrosis failed to spread along some streets.

During the peak years of loss from each disease, Dutch elm disease killed approximately four to five times as many elms as did phloem necrosis. The peak of elm deaths from Dutch elm disease occurred over 5 years, while the peak of elm deaths from phloem necrosis occurred in two periods, the first lasting 4 years and the second 2 years. Following these peak periods the numbers of elms affected annually by each disease decreased rapidly, for over 90 percent of the 1944 elm population of Champaign-Urbana had been killed by 1960.

In some blocks and along some streets all elms were killed within 3-5 years by one or both diseases. All 36 elms in the 700 block of South Lynn Street in Champaign were killed by phloem necrosis in 3 years, and 28 of 29 elms in the 700 block of West Michigan Avenue in Urbana were killed by Dutch elm disease in 5 years.

Where both diseases were present, Dutch elm disease killed more trees than did phloem necrosis. Dutch elm disease tends to kill trees more rapidly than does phloem necrosis. Most elms affected by Dutch elm disease die in the same year in which foliage wilt appears, but most elms affected by phloem necrosis die in the year following the appearance of foliage wilt. Also, more phloem necrosis-affected elms show wilt symptoms in September than show them in June, while more Dutch elm disease-affected trees show wilt symptoms in June than show them in September. Some elms die during the winter without any visible foliage wilt. While each disease may contribute to these winter deaths, it seems likely that Dutch elm disease is mainly responsible.

Some elms that first showed symptoms of phloem necrosis subsequently showed symptoms of Dutch elm disease. As the number of elms killed by Dutch elm disease increased, the num-

ber of phloem necrosis-affected elms subsequently affected by Dutch elm disease increased. This fact suggests that as the supply of Dutch elm disease inoculum increases, more phloem necrosis-affected elms are invaded by the Dutch elm disease fungus. Also, the greater the number of elms infested with bark beetles, the greater the chances for the spread of the Dutch elm disease fungus.

Although some elms affected by phloem necrosis in June showed Dutch elm disease symptoms in September, in most cases Dutch elm disease symptoms did not appear until the year following the appearance of phloem necrosis symptoms. Only phloem necrosis-affected elms that die slowly during one or more growing seasons can be subsequently affected by and show symptoms of Dutch elm disease. Phloem necrosis-affected elms that are subsequently affected by Dutch elm disease appear to be killed by Dutch elm disease and not by phloem necrosis (Campana & Carter 1955).

The cycle of elm deaths from Dutch elm disease probably was affected only slightly, if at all, by the presence of phloem necrosis. This conclusion is based on the fact that elm deaths from Dutch elm disease built up to a peak more rapidly than did elm deaths from phloem necrosis. During the 5-year period 1955-1959 more than eight times as many elms were killed by Dutch elm disease as were killed by phloem necrosis. However, the cycle of elm deaths from phloem necrosis was greatly shortened by the presence of Dutch elm disease; Dutch elm disease killed 78.4 percent of the elms, while phloem necrosis killed only 21.2 percent.

SUMMARY

In the 29-year study reported here, data were recorded on the spread of and losses caused by elm phloem necrosis and Dutch elm disease in a mu-

nicipal area which had no community-wide control program for either disease.

Phloem necrosis appeared in Urbana in 1944, when two trees were affected. Dutch elm disease did not appear until 1951, when one tree was affected. The initial spread of phloem necrosis was not influenced by Dutch elm disease, since Dutch elm disease was not present during that period. Each of the 14 elms that contracted phloem necrosis from 1945 through 1948 was scattered at random beyond root-grafting distance of other diseased trees, and each tree represented a separate infection center. Phloem necrosis spread rapidly along some streets, killing all 36 elms in one block within 3 years.

The early spread of Dutch elm disease was influenced by phloem necrosis. Phloem necrosis-affected elms can harbor the Dutch elm disease fungus, and the elms killed by phloem necrosis were heavily colonized by the smaller European elm bark beetle, vector of the Dutch elm disease fungus. Many of the phloem necrosis-affected elms were not removed before the bark beetles emerged.

Dutch elm disease spread rapidly to elms in areas where phloem necrosis was abundant, and it also affected scattered elms located well away from phloem necrosis-affected elms. However, of 164 elms having Dutch elm disease in 1953 only 41 were in scattered locations away from phloem necrosis-affected trees.

Dutch elm disease, like phloem necrosis, spread rapidly to elms along some streets. Twenty-eight elms were killed by this disease in one block in 5 years. Of 47 elms in six blocks of one street, 17 were killed by phloem necrosis in 2 years and 30 were killed by Dutch elm disease in 5 years. However, Dutch elm disease was present for 2 years before phloem necrosis appeared. Phloem necrosis and Dutch elm disease were spread mainly by their respective insect vectors in this area, because 39 of the 47 elms were beyond root-

grafting distance of previously diseased trees.

Some phloem necrosis-affected elms subsequently became infected with the Dutch elm disease fungus and showed typical symptoms of Dutch elm disease before dying. The number of phloem necrosis-affected elms that subsequently became affected by Dutch elm disease increased as the incidence of Dutch elm disease increased.

The greatest number of elms affected by phloem necrosis in 1 year was 555 trees in 1952, 8 years after the disease was discovered in this area. The greatest number of elms affected by Dutch elm disease was 2,116 trees in 1957, 6 years after the disease was discovered here. Of the original population of 14,103 elms, 2,994, or 21.23 percent, were killed by phloem necrosis in 29 years. Dutch elm disease killed 11,062,

or 78.44 percent, in 22 years. Both diseases killed 14,056, or 99.67 percent, of the elms. Dutch elm disease had a greater effect on the residual elm population, since it killed more than three times as many elms as did phloem necrosis.

More elms showed symptoms of phloem necrosis in the September survey than showed such symptoms in the June survey. The reverse was true of elms having Dutch elm disease. Following the appearance of wilt symptoms, elms affected by Dutch elm disease tended to die more rapidly than did elms affected by phloem necrosis. Most elms that had Dutch elm disease died in the growing season in which foliage wilt appeared, while most elms that contracted phloem necrosis died in the year following the appearance of foliage wilt.

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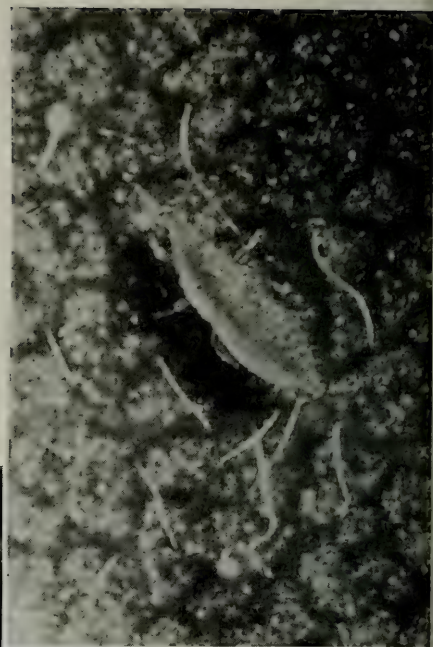
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Thomas C. Vance is employed by the Illinois Department of Conservation as a Site Interpretive Specialist at Lincoln Log Cabin State Park, Lerna, Illinois.



Frontispiece.—Larva I (lower left) and larva II (upper right) of *Sericothrips pulchellus* Hood on its host, wafer ash (*Ptelea* sp.). (Photographs by Lawrence S. Farlow)

Larvae of the Sericothripini (Thysanoptera: Thripidae), with Reference to Other Larvae of the Terebrantia, of Illinois

Thomas C. Vance

The morphology and taxonomy of the immature stages of the Thysanoptera have received minimum attention in North America. Significant contributions on the larvae of thrips have been made in Europe, East Asia, and North Africa (Priesner 1926a, 1926b-1928, and 1960) and in India (Jagadish & Ananthakrishnan 1972), and these studies constitute the basis of our knowledge. In the United States most of the descriptions of the immature stages are found in accounts of the life histories of economically important thrips.

This report deals mainly with the second-stage larvae, especially the known forms belonging to the tribe Sericothripini as represented in Illinois, and includes a comparison of the larval characteristics of many of the genera of the suborder Terebrantia that are found in the same region. Larval characteristics were used to substantiate the classification formerly based on adult features and to interpret the phylogeny of this insect order. A special study on the life history of *Sericothrips variabilis* (Beach) was included to provide an example of the bionomics of a common species.

References to the literature, with few exceptions, terminated in 1971 when this report was submitted as a Master of Science thesis to the Department of Entomology, University of Illinois, Urbana.

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The manuscript was edited for publication by Robert M. Zewadski, Associate Technical Editor, Illinois Natural History Survey, and reviewed by Dr. Bruce S. Heming, Associate Professor, University of Alberta, and Dr. Lewis J. Stannard, Jr., Illinois Natural

History Survey Taxonomist and Professor of Entomology, University of Illinois. The typing and proofreading of the manuscript were done by Mrs. Bernice Sweeney and Mrs. Grace Finger, Illinois Natural History Survey.

MATERIALS AND METHODS

During this study about 500 immature thrips were examined. In addition, diagnostic features were analyzed from descriptions of immatures in the literature, the reference being cited in each case. Repositories and institutions are identified in the Material-Examined sections by these abbreviations:

INHS = Illinois Natural History Survey collection

USNM = United States National Museum (National Museum of Natural History, Smithsonian Institution)

Three methods were used in collecting immature thrips. Large plants were sampled with a black sweep net (to make the light-colored immatures more visible), the thrips being recovered from the net with the aid of a hand lens and a small camel hair brush. Branches were shaken over a piece of cardboard or other material from which the thrips were recovered. Small host plants were sampled by examining individual leaves, and the thrips were removed directly from the leaf surfaces.

The preserving solution used was AGA (eight parts 95-percent ethanol, five parts distilled water, one part glycerine, and one part acetic acid), which kept the body soft and facilitated spreading of the appendages. For storage beyond 4 weeks, thrips were transferred to 70-percent ethanol.

Both Canada balsam and Hoyer's medium were used in making whole mounts. Canada balsam is a permanent mounting medium (Hartwig 1952; Priesner 1960; Stannard 1968), which preserves the color and features of thrips well, but it is difficult to use and much

time is required to make good preparations. Further, because of dehydration and accompanying brittleness, specimens can be damaged during mounting in Canada balsam, and small setae, microtrichia, cuticular sculpturing, and areas of light brown coloration often are obscured.

Hoyer's is easier to use and renders visible many diagnostic features not usually seen on specimens mounted in balsam. Unfortunately, Hoyer's, a water-base medium, usually crystallizes within a few years. Specimens for the permanent collection, therefore, were mounted in Canada balsam, but some of each series were mounted in Hoyer's medium for temporary study.

Balsam mounts were prepared in a manner similar to that described by Heming (1969). Larvae and adults were transferred from AGA to 70-percent ethanol and were then passed successively through 95-percent ethanol, absolute ethanol, and absolute ethanol and clove oil, remaining in each solution for about one-half hour. Specimens were then placed in a small Syracuse watch glass containing pure clove oil; when each sank to the bottom, it was transferred to a slide. Clearing in 10-percent KOH or NaOH was usually unnecessary for immatures except to dissolve the excessive amounts of fat body found in some larvae.

In mounting, each thrips was placed ventral side up in a small drop of dilute balsam on a cover slip held in place on a small cardboard stage. The appendages were spread, and two chips of cover glass were added to the balsam. These chips prevent crushing of the specimen by the cover slip as the balsam dries. A small drop of balsam was placed in the center of a microscope slide, and the slide was inverted and placed gently upon the cover slip. When the slide was lifted and turned right side up, the cover slip and specimen adhered to it. Slight pressure applied to the cover slip with

an insect pin spread the appendages farther.

Whole mounts in Hoyer's medium were prepared in the same way, but the dehydration schedule was omitted. Most Hoyer preparations in the Survey collection deteriorated after a few years, even when ringed with Zut Slide Ringing Compound (Bennett's Paint Products, Salt Lake City) or clear fingernail polish. However, some preparations ringed with fingernail polish have remained in good condition for more than 20 years, indicating that efficient ringing compounds might prove successful in preserving Hoyer mounts.

Bright-light microscopes were used throughout this study except when minute structures, such as microtrichia, were being observed, for which work phase-contrast microscopes were employed.

ANALYSIS OF CHARACTERS

According to Priesner (1960) "the shape of the antennal segments, the sculpture of the body cuticle, the chaetotaxy, and last but not least, the colour, are important" in taxonomic study of larval thrips. These characters and certain others were the principal ones used in this investigation. Many characters varied with the stage of larval development, particularly color, many body dimensions, and cuticular sculpturing, which vary with growth and instar. Color also varies with the type of food consumed by the larvae. Different characters have been used in this study according to the taxonomic level concerned. In classifying thrips larvae at the family level, the form and shape of the antennal segments and the presence or absence of modified spines on the ninth abdominal tergite are important in making distinctions. At the subfamily level, the form of certain antennal segments is important. Many characters at the tribal level were found to intergrade, but certain features could generally be assigned to each tribal

group. Members of subtribal groups tended to exhibit a greater degree of similarity and could be assigned to the proper group with less difficulty.

The greatest stabilization of characters occurs at the genus level. Most genera are sharply delimited, and even closely related genera usually exhibit diagnostic differences. One exception occurred in the tribe Thripini in which the larvae of the *Frankliniella-Thrips-Taeniothrips* complex are quite similar. Important generic characters include cuticular sculpturing; microtrichia; setal type, length, and placement; coloration; and proportions and features of the antennal segments.

Little distinction was found at the species level, closely related species often being nearly alike in form. Species differences that were found include the length and proportions of the body setae, brown sclerotized areas, setal basal rings, and cuticular and hypodermal coloration in mature larvae. Ward (1968) found that slight consistent differences are present in larvae of several closely related species of *Thrips* and that, despite their subtlety, these characteristics can be used to separate these species with confidence.

Most of the characters mentioned above apply to second-instar larvae; in first-instar larvae few diagnostic characters occur at the generic level and none were detected at the specific level. At the family and subfamily levels first-instar larvae may be recognized by the same antennal characters distinguishing second-instar larvae. At the tribal and subtribal levels the pattern of microtrichia on the antennae and general body and antennal features are useful in making distinctions.

The prepupal and pupal instars show little interspecific variation. According to Priesner (1960), the only distinguishing characters are the presence or absence of cuticular spines near the apex of the abdomen and the shape of the antennae. The taxonomic value of these

features above the species level may be questionable, since Priesner (1960) reported one species of *Taeniothrips* with spines and another species of the same genus without them.

COLOR

Four types of coloration occur in thrips larvae: (1) that of the internal organs and body contents, (2) that of the cuticle, (3) that of underlying hypodermal pigmentation, (4) and areas of brown sclerotization on the cuticle surface. Because color varies with the degree of larval development, it is best to deal only with fully mature larvae.

The colors of internal organs and body contents depend upon the food ingested. Phytophagous larvae often appear green due to the ingestion of chlorophyll, and predacious larvae may assume the color of the prey ingested. Such colors are usually leached out during the mounting process and are practically useless for taxonomic purposes.

Cuticle color among specimens of the same species varies from white to yellow to orange. These pigments can be affected by the mounting media used, and are leached out with prolonged storage in alcohol.

Underlying hypodermal pigmentation is usually not affected by mounting media but does vary greatly even in the members of a series of specimens. Some species never show hypodermal pigmentation, while in others it is usually present in some members of a series of specimens. Hypodermal pigmentation is susceptible to leaching with prolonged storage in alcohol although at a slower rate than is cuticular coloration.

Brown sclerotized areas, such as certain antennal segments, areas of the head and thorax, and areas of the terminal abdominal segments, are the most dependable color features. Distinctive brown sclerotized areas are particularly valuable in the identification of many species of the Helio-

thripinae, Anaphothripini, and Chirothripini. This brown color does not vary much within a species, is not leached with prolonged storage in alcohol, and is not affected by mounting media although these light brown areas may be difficult to see in balsam.

ANTENNAE

Antennal features are the most reliable characters in the taxonomy of larval thrips. Lengths of segments and the number of annulations present are important at the family and subfamily levels, whereas the shapes of the segments and the nature of their annulations and microtrichia can be diagnostic of genera and higher groups. The microtrichia of antennal segments III and IV and the shapes of the terminal segments are often diagnostic in first-stage larvae of certain groups. Larval members of the Sericothripini, for example, tend to have narrowed, tapering, seventh antennal segments and dense, random microtrichia on segment IV. However, members of some other tribes have broader seventh segments, and few have microtrichia on segment IV except on the annulations.

Antennal sense cones are of diagnostic value at the generic and higher levels. The length of sense cones in adult Thysanoptera often varies, but in the larvae it seems fairly stable. In general, the primitive families (Aeolothripidae, Merothripidae, and Heterothripidae) and the tribes Chirothripini and Thripini tend to have shorter sense cones, and the Anaphothripini, Sericothripini, and Dendrothripini have longer ones. The sense cones on segments IV, V, and VI are the best developed and therefore are used for taxonomic analysis.

The entire antennae of some genera are diagnostic (such as those of *Chirothrips*, which has greatly reduced antennae); features of the entire antennae, however, often show little differentiation at the generic level.

HEAD AND PRONOTUM

The shape and size of the head and pronotum are distinctive and diagnostic of certain genera of thrips larvae. These features include the ratio of length to width, shape, size of eye facets, degree of bulging of the eyes, and degree of constriction at cheek margins. Small, nonbulging eye facets occur in the Chirothripini, and construction of the cheeks seems to be characteristic of the Heliothripinae and some Anaphothripini.

Problems associated with the head and pronotum include distortion due to pressure from the cover slip and differences in their degree of development within the larval stage.

TERMINAL ABDOMINAL SEGMENTS

The shape of the terminal abdominal segments differs between the suborders Terebrantia and Tubulifera. In the Thripini and in *Anaphothrips* a posterior comb is present on abdominal segment IX. According to Priesner (1960), each species has a characteristic form of this comb.

SETAE

The type and length of body setae are important features in larval differentiation. Setae vary in length and type above the generic level; however, they are useful in the diagnoses of genera. Setal types, as listed by Priesner (1960:66-67), are: pointed, lanceolate, blunt or rounded, knobbed, funnel-shaped, forked or fringed, and spoon-shaped or fanned. Their lengths may vary from less than 5 μm up to 70 μm , and they may be slender or stout. Each genus has characteristic types and lengths of setae.

Setae differ in their widths and lengths between species, and certain setae differ in their proportionate lengths. The degree of development of the brown rings at the bases of the

setae can be important diagnostic features. Some variation in the setae occurs between individuals; the lengths, however, do not change with the degree of development.

CUTICLE

The presence and nature of cuticular pustules and cuticular microtrichia provide good diagnostic characters at the generic and subtribal levels. Microtrichia are long to short, depending on the species. Short microtrichia are almost invisible when viewed through a light microscope and appear as a stippling effect. They are sparsely to densely scattered over the integument. Pustules are minute to large, depending on the species, and usually each pustule bears one microtrichium although the large pustules of the Anaphothripini and Heliothripinae lack microtrichia.

Cuticular features which are stable at the generic level present some problems. Small pustules and microtrichia are often difficult to see in balsam mounts and can be distorted by the mounting process. Also, cuticular sculpturing varies with the degree of larval development and abdominal distension.

METAMORPHOSIS

In the Terebrantia there are usually four immature stages, the first- and second-instar larvae, the prepupa (propupa), and the pupa. In the Tubulifera, by contrast, an additional pupal instar occurs, resulting in a total of five stages. Larval stages lack wings or wing pads and have free antennae, and active movements and feeding take place. The prepupal and pupal stages are quiescent and do not feed. Their antennae lack segmentation and are directed forward in prepupae and are bent back dorsally (Terebrantia) or laterally (Tubulifera) along the head in pupae. Wing pads are usually present in prepupae and pupae of the Terebrantia but only in the pupal stages of the Tubulifera. Each stage is terminated

by a molt, with the exuviae usually left on the leaf surface.

Thrips are usually recognized as exopterygote insects and are placed with the hemipteroid orders even though their postembryonic development more closely resembles the holometabolous transformations found in the Endopterygota. This intermediate type of development in the Thysanoptera has caused considerable controversy, some authors calling the immatures nymphs and others calling them larvae and pupae. Takahashi (1921) even proposed the term "Remetabola" for thysanopteran metamorphosis.

Recent histological studies on the postembryonic development of the Thysanoptera have provided insights into the problem. Davies (1961) found that the development and adult morphology of the female reproductive organs of *Limothrips cerealium* showed similarities to the exopterygote insects but that their delayed development recalled endopterygote morphogenesis. This conclusion is supported by Heming (1970) in a similar study on *Frankliniella fusca* (Hinds) and *Haplothrips verbasci* (Osborn). Davies (1969) studied the metamorphosis of the skeletal musculature of *L. cerealium* and found many details of myogenesis in the pupae of thrips to be similar to those in the pupae of endopterygote insects. He stated that "thysanopteran ontogeny shows histological changes at least as great as those in the holometabolous metamorphosis of many Endopterygota and these quiescent instars are perfectly entitled to rank as pupal stages." Davies further hypothesized that the holometabolous type of metamorphosis in the Thysanoptera developed independently of that of the Endopterygota and speculated about the selective value of two or three pupal stages in the Thysanoptera when only one is usually necessary for similar transformations in the Endopterygota.

LIFE HISTORY OF SERICOTHRIPS VARIABILIS (BEACH)

S. variabilis was the first species of *Sericothrips* described in North America (Beach 1896) and is one of the most common in the eastern states. It occurs abundantly on soybeans and other legumes, but its life history and the economic damage it causes are largely unknown.

Life-history studies have been made on several economically important thrips, the most complete being those of Horton (1918) on *Scirtothrips citri* (Moulton), Bailey (1933) on *Caliothrips fasciatus* (Pergande), and Ghabn (1948) on *Thrips tabaci* (Lindeman). Other accounts by Bourne (1926), Davidson & Bald (1930), Foster & Jones (1915), McKenzie (1935), Rivnay (1935), Russell (1912), Sakimura (1932), Schopp (1936), Watts (1934), and White (1916) are more brief. Bailey (1938) summarized and compared the life histories of several thrips of economic importance in California. Rearing methods are described by Bailey (1932 and 1933), Rivnay (1935), and Callan (1947).

The following data on *S. variabilis* are intended to provide information on the development of the immature stages, the effects of temperature and photoperiod, the site of pupation, mating, and predators, and an assessment of the economic importance of the species.

METHODS

Two types of rearing containers were used. The first was a covered plastic petri dish (35 mm in diameter and 10 mm deep) set vertically in a wooden rack. A soybean leaf was trimmed to fit into the dish with its stem extending through a hole in one side of the dish and into a vial of water below.

The second rearing container was a 100- x 15-mm covered glass petri dish

containing two soybean leaves and a piece of filter paper which was moistened daily. Larvae and adults were collected from soybeans on the South Farm of the University of Illinois, Urbana.

Rearing was done at controlled temperatures of 21.0°, 26.5°, and 32.0° C under constant light and at 22.0° C under an 8-hour-per-day light photoperiod. Two cultures were confined at each temperature. One culture was started with eggs already present in the leaves. A second culture was started with 10 adults. The number of larvae at each stage of growth was recorded twice daily between 0800 and 0900 hours and between 1600 and 1700 hours.

Data were tabulated and analyzed by recording the duration of each immature stage and computing each mean. Further analysis included the calculation of the standard error of the mean and *t* tests at a significance level of 0.01.

The site of pupal development was determined by examining for pupating thrips field samples of soil collected from beneath soybean plants at depths of 1 inch (25.4 mm) and at 4–5 inches (101.6–127.0 mm). Soil was placed in the lower end of a glass petri dish held at a 45° angle. Soybean leaves were set upright in the dish with the stems resting on the soil. Larvae present on the leaves could therefore drop or crawl to the soil when ready to pupate.

Sticky traps were set in the field to determine how the second-stage larvae reach the ground. Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan) was placed in 1-inch (25.4-mm) bands 6 inches (152.4 mm) from ground level around and directly on the stems of 12 soybean plants to trap any larvae crawling down the stems. Two 12-x 18-inch (304.8-x 457.2-mm) cardboard sheets covered with Tanglefoot were placed on the ground beneath the

plants at least 6 inches (152.4 mm) from the stems to catch any larvae dropping from the leaves.

FIRST-INSTAR LARVA

The mean duration of the first instar of *S. variabilis* larvae reared at 22.0° C with an 8-hour light photoperiod per day was 73.49 ± 7.32 hours. The mean body length of the cultured immatures of this instar varied from $560 \pm 80 \mu\text{m}$ for the early larva I to $720 \pm 70 \mu\text{m}$ for the late larva I. The early larva I has a narrow, tapering abdomen and a disproportionately large head and legs (Fig. 7a). As feeding takes place, the body becomes distended due to increases in the sizes of the internal organs, particularly the fat body (Fig. 7b). Cuticular color changes from white in the early larva I to yellow in the late larva I, and ingested chlorophyll often gives the body a green color.

The setae are short and narrowly fanned, setal pair P7 is lacking, and abdominal segment IX has three or four pairs of setae. (The setal and segmental numbering system used in this report is shown in Fig. 6.) Priesner (1958) speculated, but Ghabn (1948) had proved, that the male larva I has three pairs of setae on segment IX (two dorsally and one laterally), whereas the female has four pairs of setae on this segment (two dorsally, one laterally, and one ventrally). The sexes can be determined by these setal arrangements. Antennal segment IV is covered with random microtrichia, and segment VII is tapered apically.

Soon after hatching, the larva begins feeding, never moving far from the hatching site and often hiding in the angles of the larger veins on the lower leaf surface. The larvae are active and move about quickly when disturbed. In late larvae I the old cuticle becomes light gray. It splits dorsoventrally, the head and thorax are pushed out, and the antennae and legs are pulled free.

The exuviae is pushed partly down the abdomen by the hind feet, and the remainder of the abdomen is pulled free by forward pressure exerted on the leaf surface by the feet. About 4 minutes are required for this process.

SECOND-INSTAR LARVA

The mean duration of the second instar of *S. variabilis* larvae reared at 22.0° C under an 8-hour light photoperiod per day was 91.30 ± 10.44 hours. The mean body lengths of the cultured immatures of this instar varied from $910 \pm 60 \mu\text{m}$ for the early larva II to $1,030 \pm 50 \mu\text{m}$ for the late larva II. A newly molted larva has a narrow abdomen and thorax and a disproportionately large head and legs (Fig. 7c). As the larva feeds, the abdomen, particularly, and the thorax become distended (Fig. 7d). The cuticular color changes from white in the newly molted larva to orange, often with red hypodermal pigmentation, in the late larva II (although the red pigmentation was not observed in laboratory-reared larvae). Green body coloration due to ingested chlorophyll was predominant in many larvae.

The setae are long and widely fanned, appearing proportionately longer in the early larva II because the lengths of the setae remain unchanged throughout the larval stage. Setal pair P7 is present, and abdominal segment IX has five or six pairs of setae. Sex was determined by following Priesner (1958) on the number of setae on segment IX. Those larvae with five pairs of setae (two dorsally, two laterally, and one ventrally) were presumed to be females, and those with six pairs of setae (two dorsally, two laterally, and two ventrally) were presumed to be males. Priesner ignored one pair of lateral setae (A3 in this study) because they were greatly reduced, and gave the setal counts as four and five pairs. However, A3 is not reduced in larvae of certain genera (e.g., *Aeolothrips*,

Merothrips, and *Heterothrips*), and for the sake of uniformity, this pair of setae was included in all setal counts here. The color of the setae are white immediately following the molt (sometimes making newly molted second-stage larvae easily confused with mid-first-stage larvae) but soon become sclerotized and turn brown. Antennal segment IV has microtrichia only on the annulations.

Second-instar larvae feed on the leaf surface and occasionally hide in crevices. In nature they are almost always found on the undersides of leaves, but they also occur on the upper sides in laboratory cultures. Near the end of the larval stage, the larvae drop to the ground and enter the soil for pupation.

PREPUPA

The mean duration of the prepupal stage of *S. variabilis* reared at 22.0° C under an 8-hour light photoperiod per day was 22.00 ± 2.38 hours. The mean body length was $1,180 \pm 80 \mu\text{m}$. Changes in size are imperceptible during the prepupal stage. The color is predominantly orange; wing pads are present, reaching posteriorly to the second abdominal segment; the antennae are indistinctly segmented, protruding anteriorly from the head; and the setae are simple and short. Abdominal segment IX lacks the cuticular spines found in the prepupae of some genera (Fig. 7e).

Female prepupae possess two pairs of short lobes arising ventrally on abdominal segments VIII and IX; these are the buds of the ovipositor valves. Male prepupae lack these structures (Priesner 1960).

The prepupal period is normally passed in the soil, but in laboratory cultures where soil was unavailable, prepupation readily took place on the leaf surface. Under laboratory rearing conditions, the prepupae were quies-

cent and nonfeeding and were usually hidden in crevices between the large leaf veins; activity was observed only when the prepupae were disturbed or threatened.

PUPA

The mean duration of the pupa stage of *S. variabilis* reared at 22.0° C under an 8-hour light photoperiod per day was 74.00 ± 2.83 hours. The mean body length was $1,040 \pm 60 \mu\text{m}$. No change in size was noted during pupal development. The color is predominantly orange during this stage. The wing pads reach the sixth abdominal segment, and the antennae are recurved along the dorsum of the head. The setae are simple and pointed and longer than in the prepupa. Abdominal segment IX lacks the cuticular spines found in the pupae of some genera (Fig. 7f).

The ventral lobes on segments VIII and IX in female pupae are longer and better developed than those found in female prepupae. Male pupae have a bluntly triangular production ventrally at the hind margin of segment IX.

Pupal development took place in the upper inch (25.4 mm) of soil beneath soybean plants or in the soil provided in laboratory cultures. In cultures where soil was not available, pupation readily took place on the leaf surface, the quiescent, nonfeeding pupae being hidden between the larger leaf veins.

ADULT

Adults of *S. variabilis* may be distinguished from those of other species of the genus in Illinois by the following combination of characteristics (Stanard 1968): each fore wing with two sharply defined crossbands; the pronotal blotch completely dark in contrast to the rest of the pronotum and deeply incised medially and posteriorly by yellow; anterior pronotal striations closely spaced; several abdominal segments dark brown.

Adults are quite active and, when disturbed, dart about or jump rapidly. Adults seldom survive long in a culture dish when transferred from field samples but remain alive for up to 4 or 5 days when reared in the laboratory.

EFFECT OF TEMPERATURE AND PHOTOPERIOD ON DEVELOPMENT

Both temperature and photoperiod affected the durations of the immature stages of *S. variabilis* (Table 1 and Fig. 1). Under constant light the durations of the stages were about 27 percent longer than that required at about the same temperature under an 8-hour-per-day light photoperiod. Temperature and durations of the stages were inversely correlated, the most rapid de-

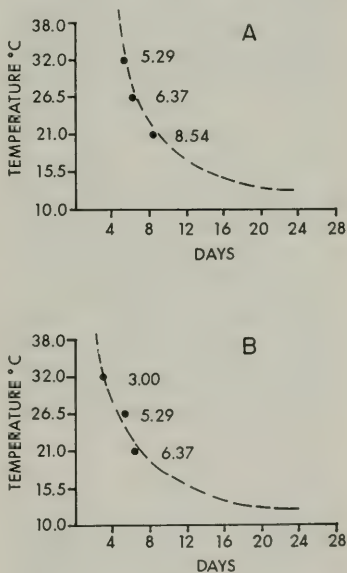


Fig. 1.—Growth curves of immature stages of *Sericothrips variabilis* reared in the laboratory. **A**, mean duration of the larva I and larva II stages, combined, at various constant temperatures. **B**, mean duration of the prepupal and pupal stages, combined, at various constant temperatures.

Table 1.—Duration of immature stages of *Sericothrips variabilis* at different temperatures and photoperiods. The numbers of insects observed are in parentheses.

Temperature (in Celsius) and Photoperiod	Mean Hours of Duration			
	Larva I	Larva II	Prepupa	Pupa
22.0°, 8-hour photoperiod	73.49 ± 7.32 ^a (23)	91.30 ± 10.44 (24)	22.00 ± 2.38 (2)	74.00 ± 2.83 (2)
21.0°, constant light	97.33 ± 4.68 (6)	107.33 ± 6.99 (8)	35.00 ± 7.57 (4)	...
26.5°, constant light	65.33 ± 6.11 (5)	87.34 ± 14.09 (14)	29.33 ± 6.11 (3)	...
32.0°, constant light	58.67 ± 2.83 (7)	68.00 ± 6.85 (11)	16.00 ± 4.00 (7)	56.00 ± 6.20 (6)

^a Standard error. Standard *t* tests computed at a probability level of 0.01 showed all means to be significantly different except for these pairs:

Larva I: 22.0° and 26.5°, 26.5° and 32.0°.

Prepupa: 22.0° and 21.0°, 22.0° and 26.5°, 22.0° and 32.0°, 21.0° and 26.5°.

velopment taking place at 32.0° C. At 26.5° C the mean duration of immature stages was increased by about 41 percent, and at 21.0° C the mean duration was increased by about 81 percent over the time required at 32.0° C. The least mortality occurred at 26.5° C, indicating that this might be the optimum of the three temperatures for the development of the immature stages of this insect.

S. variabilis requires more time for development of the immature stages than does *Thrips tabaci* Lindeman and *Taeniothrips simplex* Morison; the same time as *Scirtothrips citri* (Moulton), *Caliothrips fasciatus* (Pergande), and *Frankliniella tritici* (Fitch); and less time than *Taeniothrips inconsequens* (Uzel), *Heliothrips haemorrhoidalis* (Bouché), *Liothrips vaneecki* Priesner, and *Hercinothrips femoralis* (Reuter) (Bailey 1938).

SITE OF PUPATION

Studies on the biology of many pest thrips indicate that late second-stage larvae drop to the ground and pupate in the soil. *S. variabilis* also pupates in the soil, as shown by the results of the field tests conducted during this study. Pupae were found 1 inch (25.4 mm) below the surface in soil samples taken beneath soybean plants. Each

pupa was located in a small chamber in the middle of a dirt particle one-half inch (12.7 mm) in diameter. In the experiment designed to discover how the larvae reach the ground, no immatures were caught in sticky traps placed around the stems of the plants. In contrast, on the sticky sheets beneath the plants 10 late second-stage larvae and three adults were found on one and 5 late second-stage larvae and two adults on another, indicating that the larvae drop to the soil from the leaves before pupation begins.

Information concerning the site and conditions of pupation of some thrips is given by Bailey (1933), and Parrot (1911) gives information on the use of sticky traps in locating pupation sites of certain of the Terebrantia.

MATING

The complete mating process was observed in two adults that had emerged in a laboratory culture. Seemingly the male first became aware of the female when he approached within about one-half inch (12.7 mm) of her. He immediately ran, caught her, and mounted her dorsally. The female began twisting the abdomen about 2 seconds after the male had mounted. Three attempts were then made to make genital contact, the third being successful. The

time lapse to this point from the initial mounting was 22 seconds. Two seconds after making genital contact, the male dismounted while maintaining genital contact, and both male and female remained motionless for 51 seconds facing in opposite directions. Contact was then broken, and each went in a separate direction.

PREDATORS

Three predators were found in association with *S. variabilis* in the laboratory cultures: *Aeolothrips fasciatus* (Linneaus) (Thysanoptera: Aeolothripidae), *Orius insidiosus* (Say) (Heteroptera: Anthocoridae), and mites of the family Phytoseiidae (Acarina).

Several *A. fasciatus* immatures appeared in the cultures and developed along with *S. variabilis*. The *Aeolothrips* larvae were observed feeding on *Sericothrips* larvae on three occasions. One *Aeolothrips* reached maturity in the culture dish, as did others reported on by Robinson, Stannard, & Armbrust (1972).

Phytoseiid mites were observed carrying dead *Sericothrips* larvae on two occasions but were not observed actually feeding. According to Chant (1958) and Chant & Fleschner (1960), phytoseiid mites can be important predators of certain phytophagous mites, but little is known of their predation on thrips or other insects. In laboratory cultures these mites survived well and could be reared easily with thrips for study on the interaction between the two.

Nymphs of *O. insidiosus* were observed in association with *S. variabilis* on many samples brought from the field and were found several times in the laboratory cultures. Although no predation was observed, it is probable that these anthocorids were feeding on thrips larvae. Borror & DeLong (1964) reported *O. insidiosus* as predatory on various species of thrips and other in-

sects, and Bailey (1933) showed that another species, *O. tricolor* White, is a predator of the bean thrips, *Caliothrips fasciatus*. The adults of *tricolor* were observed to consume about one larva an hour, the nymphs appearing even more voracious. Both nymphs and adults preferred young larvae. *O. indicus* (Reuter) feeds extensively on *Taeniothrips nigricornis* (Schmutz) (= *T. distalis* Karny) in India (Rajasekhara & Chatterji 1970).

Other predators reported by Bailey (1933) were larvae of *Chrysopa californica* (Coquillett), *Hippodamia convergens* (Guerin), *Aeolothrips kuwanai* (Moulton), and *A. fasciatus*.

ECONOMIC ASSESSMENT

Although *S. variabilis* is generally considered to be of minor economic importance, Bailey (1940) rated it as ninth in economic importance among thrips species of the conterminous United States.

In laboratory cultures immature stages of *S. variabilis* apparently caused little damage to soybean leaves, even with a population of 8-10 thrips per leaf, despite the small amount of yellowing which was evident at times.

During the latter part of the summer, many upper leaves on soybean plants in the field showed yellowing, browning, and other evidence of insect-feeding damage. This damage, however, cannot be directly attributed to thrips because a variety of other insects also feed on soybeans. Furthermore, the population levels of *S. variabilis* in the field were estimated at an average of one or fewer thrips per leaflet at each observation. At this density level little economic damage results. However, thrips damage at levels of 30-60 insects per plant (number per leaflet not stated) was reported in Maryland in July 1971 in the *Cooperative Economic Insect Report* (U.S. Department of Agriculture 1971). So far as is known,

S. variabilis does not transmit plant viruses.

Other Sericothripini of economic importance include the citrus thrips, *Scirtothrips citri*, ranked seventh among economic thrips species by Bailey (1940); the grape thrips, *Drepanothrips reuteri* Priesner, given a rating of 11 and considered of minor importance; the long-winged thrips, *Scirtothrips longipennis* (Bagnall), ranked number 20 and considered as rarely of importance; and *Echinothrips americanus* Morgan, ranked 31 and also considered rarely of economic importance.

PHYLOGENY

Interpretations of the phylogeny of the Sericothripini and the relationships of that tribe to some of the other groups in the Thysanoptera were made on the basis of larval characteristics, as presented here.

Larval characters used in assessing the relationships of the major groups of Thysanoptera were: (1) the degree of elongation of antennal segments III and IV, (2) the length of antennal segment V, (3) the presence or absence of antennal microtrichia, (4) the presence or absence of antennal annulations, (5) the tendency toward fusion of antennal segments, (6) the degree of ornateness of the setae, (7) cuticular sculpturing, (8) the presence or absence of cuticular sclerotization, (9) the pigmentation of the cuticle, (10) general body size, (11) the modification of setae into spines on abdominal segment IX, and (12) the presence or absence of a posterior comb on abdominal segment IX.

The characters used in assessing the phylogeny of the Sericothripini were: (1) the distinctness of the suture between antennal segments IV and V, (2) the density of microtrichia on antennal segment IV in larva I, (3) body size, (4) the amount of cuticular pigmentation, (5) the presence or absence of

hypodermal pigmentation, (6) the presence or absence of brown sclerotized body areas, (7) setal length, (8) the degree of setal ornateness, (9) the presence or absence and the position of setae, (10) the presence or absence of setal basal rings, (11) the density of the cuticular microtrichia, and (12) the presence or absence of cuticular pustules.

In selecting these characters and in determining their primitive and derived states, it was assumed that: (1) characters found mainly in primitive groups are primitive, and (2) characters regarded as primitive in adult Thysanoptera (Stannard 1968; Gentile & Bailey 1968) might be supposed, with reservations, to be primitive in the larval stages also. Large body size, moderately ornate and long antennal segments, greater degrees of coloration, moderately ornate setae, the presence of cuticular microtrichia, lack of body pustules, lack of a posterior comb on abdominal tergite IX, and setae modified into spines on the terminal abdominal segments were considered to be primitive features of the Sericothripini and of some other tribes of the Thripidae.

Each of the characters was assigned a value from 0 to 2 for each Illinois genus of the Terebrantia and for each species of the Sericothripini found in Illinois. A value of 0 indicates a plesiomorph or primitive condition for the character in the group or species; a value of 1, an intermediate or variable condition; and a value of 2, the apomorph or derived condition. The character states and values are summarized in Tables 2 and 4, and scores and sums are summarized for 29 genera and one family in Table 3 and for 16 species of the Sericothripini in Table 5. The sum of the values for the 12 characters gives a measure of the degree of divergence of the taxon from the primitive, ancestral stock. These values are shown graphically in Fig.

2 and 4, and the inferred phylogenies are represented in Fig. 3 and 5.

PHYLOGENY OF THE THYSANOPTERA

The Aeolothripidae have generally been accepted as representing the most primitive group because of their similarities to the more primitive Corrodentia (Psocoptera) (Stannard 1957). According to Stannard (1968), the Merothripidae and Heterothripidae are of more recent origin, and the Thripidae the most recent of the Terebrantian families. The Tubulifera, according to Stannard, evolved from a phyletic line related to the Heliothripinae of the Thripidae, the evidence being the many similarities between certain members of the two groups and the many specialized features of the Tubulifera. Gentile & Bailey (1968), however, believed that the Merothripidae and Thripidae evolved from the Heterothripidae, and Priesner (1926b-1928) felt that the Merothripidae represented a possible link between the Terebrantia and the Tubulifera because of certain intermediate features found in merothrips.

The phylogenetic and systematic status of the tribes in the family Thripidae have been much debated because of the difficulty in delimiting groups at this level. Stannard (1968) recognized the Sericothripini, Dendrothripini, and Thripini but did not separate the Chirothripini and Anaphothripini because they were difficult to categorize. Gentile & Bailey (1968) suggested a phylogenetic sequence for the tribes, from most primitive to most advanced: Heliothripini, Anaphothripini, Chirothripini, Sericothripini, Dendrothripini, and Thripini. These authors indicated that the Thripini have become specialized by degeneracy. All of these phylogenetic arrangements were derived, primarily, from studies of adult characteristics.

An interpretation of the higher Thy-

sanoptera phylogeny, based on larval characters, can be depicted as in Fig. 3.

Most larval features in aeolothripids were assumed to be primitive although lack of color and pigmentation seemed to be an advanced trait. This family is characterized by such primitive larval features as spines (modified A1 and A2 setae) on abdominal tergite IX; large body size; cuticular sculpturing lacking pustules; complete anterior and posterior tentorial arms (personal communication, B. S. Heming, 31 January 1972); antennal segments III-V elongate and segments II-VII strongly annulated, with prominent microtrichia.

From the Aeolothripidae two phyletic lines seem to have emerged: the merothripid-phlaeothripid (Tubulifera) line and the heterothripid-thripid line.

The merothripid line is characterized by the retention of a smooth cuticle; long fifth antennal segment; large body size; the loss of antennal annulations and microtrichia; complete anterior and posterior tentorial arms (personal communication, B. S. Heming, 31 January 1972); and a tendency toward the fusion of antennal segments VI and VII. The heterothripid line is characterized by the retention of antennal annulations and microtrichia; the development of cuticular pustules; small body size; the reduction of the fifth antennal segment; and, occasionally, the fusion of antennal segments VI and VII.

The merothrips are more specialized than are the Aeolothripidae in the elongation of antennal segments III-V (V remaining equal to IV), the reduction of antennal annulations, the loss of annular microtrichia, the fusion of antennal segments VI and VII, and a partial reduction of the spines on abdominal tergite IX. Merothrips retain such aeolothripid features as abdominal spines, simple setae, smooth cuticle, large body size, and antennal segment V unreduced and equal to segment IV.

Table 2.—Phylogenetically significant characters of the Thysanoptera and their character states and values.

Character Number and State	Value ^a
I Antennal segments elongated	0
Antennal segments not elongated	2
II Antennal segment V long	0
Antennal segment V reduced	2
III Antennal segments with prominent microtrichia	0
Antennal segments with microtrichia reduced	2
IV Antennal segments with prominent annulations	0
Antennal segments with annulations reduced	2
V No fusion of antennal segments	0
Fusion of certain antennal segments	2
VI Setae ornate or long	0
Setae simple or short	2
VII Cuticle without pustules	0
Cuticle with pustules	2
VIII Brown sclerotized body areas present	0
Brown sclerotized body areas lacking	2
IX Prominent cuticular and hypodermal coloration	0
Little cuticular and hypodermal coloration	2
X Body large	0
Body small	2
XI Setae on terminal abdominal segments modified into spines	0
Setae on terminal abdominal segments not modified into spines	2
XII Posterior comb lacking on abdominal segment IX	0
Posterior comb present on abdominal segment IX	2

^a An intermediate or variable state was given a value of 1.

The Tubulifera are more specialized than the Merothripidae in the total loss of antennal annulations and of abdominal spines on tergite IX, but the two groups are similar in the retention of a smooth cuticle, large body size, a long fifth antennal segment, and occasional fusion of antennal segments VI and VII.

Just as the merothripids are possibly intermediate between the Aeolothripidae and the Phlaeothripidae, so the heterothripids may be intermediate between the Aeolothripidae and the Thripidae. The heterothripids retain such aeolothripid features as annulations on abdominal segments II–VII and prominent spines on abdominal segment IX but also have characteristic thripid features, such as reduced third and fourth antennal segments, the retention of antennal annulations and microtrichia, the reduction of the tentorium, and the development of cuticular pustules. One feature that is ob-

viously intermediate in the Heterothripidae is the length of antennal segment V; in aeolothripids it is equal to the length of segment IV, and in thripids it is reduced to less than one-fourth the length of segment IV. In the heterothripids, however, antennal segment V is about one-half the length of segment IV.

The Thripidae have retained antennal annulations and microtrichia, but the length of antennal segment V has been greatly reduced, body size has become smaller, and cuticular pustules have appeared. Many features vary from a primitive to an advanced state within the group.

The family Thripidae shows considerable specialization and diversification. As the Tubulifera became specialized into a fungus-eating niche, the Thripidae diversified into a phytophagous niche and tended toward an evolutionary degeneration or simplification of many characters. Since the Thripidae

Table 3.—Character values for genera and one family of the Thysanoptera. The higher a group's total of character values, the more advanced the group is interpreted to be.

Taxon	Character ^a												Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
<i>Aeolothrips</i>	0	0	0	0	0	1	0	2	1	0	0	0	4
<i>Franklinothrips</i>	0	0	0	0	0	1	0	2	0	0	2	0	5
Phlaeothripidae	1	1	2	2	2	0	0	1	0	0	0	0	9
<i>Merothrips</i>	2	1	2	1	2	1	0	1	1	0	0	0	11
<i>Heterothrips</i>	2	1	1	0	0	0	2	2	2	1	0	0	11
<i>Caliothrips</i>	1	1	2	0	0	0	2	1	0	2	2	0	11
<i>Heliothrips</i>	1	1	2	0	0	2	2	2	1	2	2	0	15
<i>Hercinothrips</i>	0	1	2	0	0	2	2	1	2	2	2	0	14
<i>Parthenothrips</i>	1	1	2	0	0	0	2	2	2	2	2	0	14
<i>Limothrips</i>	2	1	2	2	0	1	1	0	1	2	2	0	14
<i>Chirothrips</i>	2	2	2	2	2	2	1	1	1	2	2	0	19
<i>Chilothrips</i>	2	2	2	1	0	1	2	2	0	2	0	0	14
<i>Oxythrips</i>	2	2	2	1	0	1	2	1	0	2	0	0	13
<i>Aptinothrips</i>	2	2	2	1	0	2	2	1	1	2	2	0	17
<i>Chaetanaphothrips</i>	2	2	1	1	0	0	2	2	1	2	2	0	15
<i>Anaphothrips</i>	2	2	1	1	0	2	2	0	1	2	2	1	16
<i>Echinothrips</i>	2	2	0	1	0	0	1	2	2	0	2	0	12
<i>Sericothrips</i>	2	2	0	1	1	0	1	1	1	2	2	0	13
<i>Zonothrips</i>	2	2	0	1	1	0	1	2	1	2	2	0	14
<i>Drepanothrips</i>	2	2	0	1	1	1	0	2	2	2	2	0	15
<i>Scirtothrips</i>	2	2	0	1	1	1	0	2	2	2	2	0	15
<i>Dendrothrips</i>	2	2	0	1	1	1	1	2	2	2	2	0	16
<i>Pseudodendrothrips</i>	2	2	0	1	1	1	1	2	2	2	2	0	16
<i>Leucothrips</i>	2	2	0	1	1	1	1	2	1	2	2	0	15
<i>Ctenothrips</i>	2	2	1	1	2	2	2	2	2	2	2	2	22
<i>Scotothrips</i>	2	2	1	1	2	0	2	2	2	2	2	0	18
<i>Thrips</i>	2	2	1	1	2	2	2	1	1	2	2	2	20
<i>Frankliniella</i>	2	2	1	1	2	2	2	2	2	2	2	2	22
<i>Taeniothrips</i>	2	2	1	1	2	2	2	2	1	2	2	2	21
<i>Microcephalothrips</i>	2	2	1	1	2	1	2	1	2	2	2	1	19

^a See Table 2 for characters and their states.

show a more pronounced delimitation of groups, this phyletic line probably originated earlier than did the Phlaeothripidae.

PHYLOGENY OF THE TRIBES OF THE THIRIPIDAE

As when using adult characters, delimiting tribal groups of the Thripidae is also difficult when considering larval characters. As can be seen in Fig. 2, all tribal groups except the Thripini are derived to about the same extent from primitive stock. Since each group exhibits certain specializations and evolutionary advancements, it is possible that

some of the tribes do not follow a single line of phyletic ascent but rather follow several separate lines, each being fairly independent of the others and of an origin ancient enough that many intermediate types have disappeared.

Although easily distinguished, the Sericothripini and Dendrothripini show many similarities, possibly indicating a divergence of these groups later than the divergences of most others. One feature unique to this phyletic line is the pattern of microtrichia on antennal segment IV of the first-stage larvae. The microtrichia are found randomly placed between as well as on the an-

nulations, whereas in other groups they occur mainly on the annulations and only sparsely between them.

The most primitive subfamily in the Thripidae is the Heliiothripinae. This subfamily shares with the Heterothripidae

dae the retention of annulations on antennal segments V-VII, less reduction of segment V than occurs in most thripids, an elongation of segment VII, and, in some genera, an elongation of segments III and IV (this latter feature

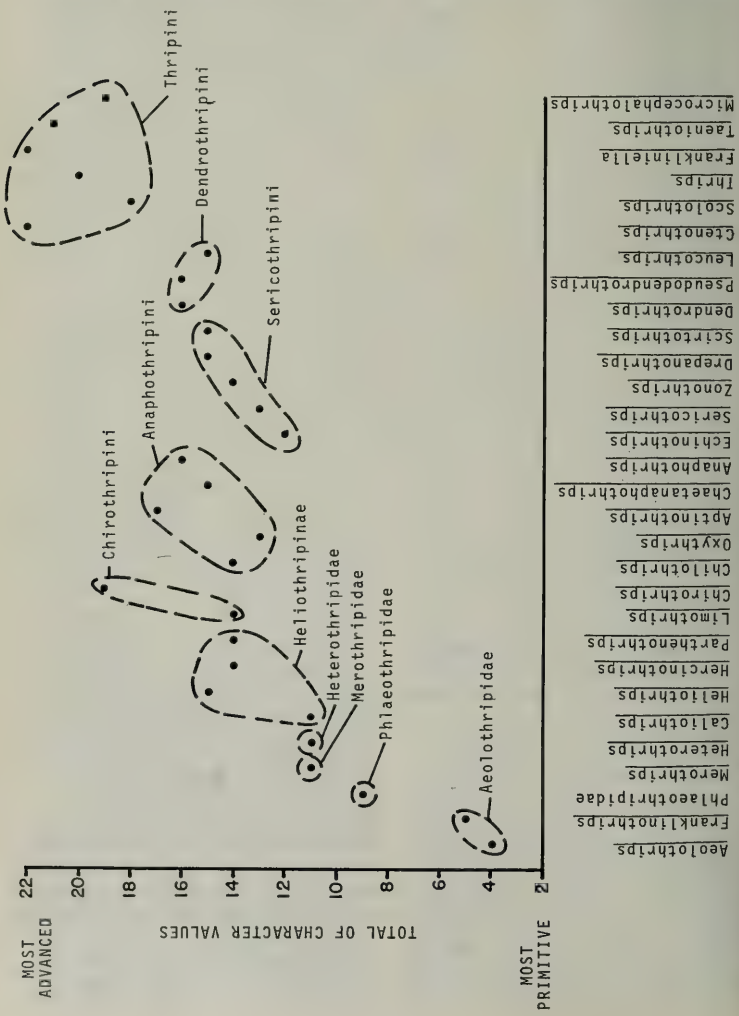


Fig. 2.—Comparison of the degree of derivation among 29 genera and one family of the Thysanoptera. These comparisons are based for each group on the total of the values of larval characters shown in Table 2 and totaled in Table 3. The higher a

reapproaching that in the Aeolothripidae). The Heliothripinae share with the Thripinae a partial reduction of antennal segment V and the loss of spines on abdominal tergite IX.

The Heliothripinae have such primitive thripid features as large pustules, brown sclerotized body areas in many species, long anal setae, and a great diversity in ornamentation.

The tribe Chirothripini shares several primitive features with the Heliothripinae. The genus *Limothrips*, like the Heliothripinae, has a reduction in the number of annular microtrichia and brown sclerotized body areas. Segment V in the antennae of first-stage larvae of *Limothrips* is elongate and has two annulations, a feature found only in more primitive groups, including the

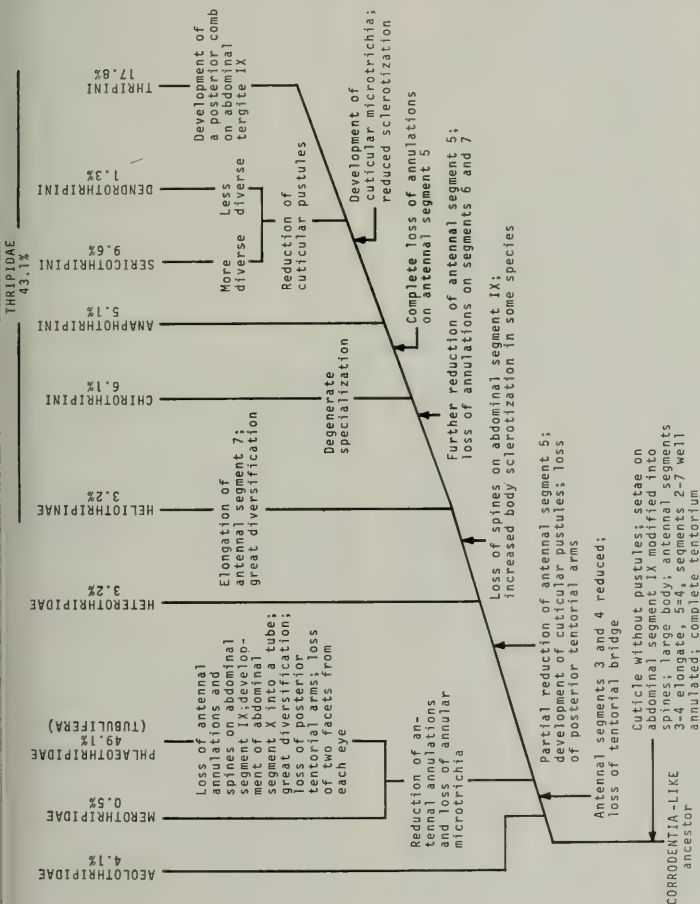


Fig. 3.—Phylogeny of the Thysanoptera, based on larval characters. This phylogeny indicates the probable origins of the major taxa and the relative proportions of the taxa in the present thrips fauna of Illinois.

Table 4.—Phylogenetically significant characters of the Sericothripini and their character states and values.

Character Number and State	Value ^a
I Antennal segment V distinct in larva I	0
Antennal segment V partially fused to segment IV in larva I	2
II Microtrichia densely placed on antennal segment IV	0
Microtrichia sparse on segment IV	2
III Large body	0
Small body	2
IV Cuticle darkly pigmented	0
Cuticle lightly pigmented	2
V Hypodermal pigment present	0
Hypodermal pigment absent	2
VI Brown sclerotized body areas present	0
Brown sclerotized body areas not present	2
VII Setae long	0
Setae short	2
VIII Setae ornate	0
Setae not ornate (simple)	2
IX Some setae reduced or lacking	0
All setae normally present	2
X Setal basal rings present	0
Setal basal rings absent	2
XI Microtrichia dense on cuticle	0
Microtrichia sparse on cuticle	2
XII Cuticle with pustules	0
Cuticle without pustules	2

^a An intermediate or variable state was given a value of 1.

Heliothripinae. The second-stage antennae of *Limothrips* are typical of those of the Thripinae.

Within the Chirothripini, *Limothrips*, with normal antennae, long knobbed setae, and brown sclerotized body areas, is most primitive. *Chirothrips* exhibits an extreme evolutionary degeneracy and specialization. Some *Chirothrips* larvae, at least, spend their whole existence within a grass floret (Watts 1965); the antennae and legs of the larvae are greatly reduced, the setae are minute and pointed, and little brown sclerotization is present.

The Anaphothripini also share many primitive traits with the Heliothripinae. Cuticular pustulation and the lack of microtrichia are very similar between the two groups, and many Anaphothripini have brown sclerotized body areas similar to those in the Heliothripinae. Genera such as *Oxythrips* and *Chiloithrips* show a modification of

certain setae on the terminal abdominal segments into setaelike spines, a condition found only in the primitive families.

The Anaphothripini have antennal segment V reduced in the first-stage larva, and have shorter antennal segments, less ornate setae, shorter anal setae, and less diversification than have the Heliothripinae.

The tribe Sericothripini is transitional between the more primitive and the more specialized tribes in the Thripidae. The Sericothripina share, in some species, several characteristics with the Anaphothripini, and the Scirtothripina with the Dendrothripini. The *annulipes* group of *Sericothrips* have such seemingly primitive features as brown sclerotized body areas, hypodermal pigmentation, large basal rings on the setae, and in *Sericothrips cingulatus* small cuticular pustules. Except for cuticular pustules these features are

Table 5.—Character values for members of the Sericothripini. The higher a group's total of character values, the more advanced the group is interpreted to be.

Taxon	Character ^a												Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
<i>Echinothrips</i>	0	2	0	1	2	2	0	0	0	2	2	1	12
<i>Sericothrips</i>													
<i>cingulatus</i>	2	0	1	0	2	0	1	0	2	0	2	0	10
<i>pulchellus</i>	2	0	1	0	0	0	1	0	2	0	2	1	9
<i>annulipes</i>	2	0	1	0	0	0	1	0	2	0	2	1	9
<i>variabilis</i>	2	0	0	0	0	2	1	0	2	0	2	1	10
<i>baptisiae</i>	2	0	1	2	2	2	2	0	2	1	2	1	17
<i>campestris</i>	2	0	1	0	2	2	1	0	2	1	2	1	14
<i>beachae</i>	2	0	1	2	2	2	1	0	2	1	2	1	16
<i>sambuci</i>	2	0	1	1	2	2	1	0	2	2	2	1	16
<i>tiliae</i>	2	0	1	1	2	2	1	0	2	1	2	1	15
<i>nubilipennis</i>	2	0	1	2	2	2	1	0	2	1	2	1	16
<i>langei</i>	2	0	1	1	2	2	2	1	2	1	2	1	17
<i>Drepanothrips</i>													
<i>reuteri</i>	2	?	2	2	2	2	2	2	2	2	1	2	21
<i>Scirtothrips</i>													
<i>niveus</i>	2	0	2	2	2	2	2	2	2	2	0	2	20
<i>taxodii</i>	2	0	2	1	2	2	2	2	2	2	0	2	19
<i>brevipennis</i>	2	0	2	1	2	2	2	2	2	2	0	2	19

^a See Table 4 for characters and their states.

usually not found in the more advanced Thripinae. The *tiliae* group of *Sericothrips* also lacks these features. The Sericothripina and Echinothripina are plesiomorphic in their ornate, fringed setae and in certain other characteristics; in the Scirtothripina, however, the setae are reduced. The Scirtothripina are smaller, lack body coloration, and have shorter setae that are only terminally funneled, all seemingly indicating a more derived condition than those found in the Sericothripina and Echinothripina.

The Dendrothripini are similar in their morphology to the Scirtothripina, indicating close phyletic relationships.

Of the tribes in the subfamily Thripinae, the Thripini is the most specialized, lacking body coloration and brown sclerotization, having reduced setal ornateness, and exhibiting a general lack of diversification. The posterior comb of abdominal tergite IX is an advanced characteristic found in several genera in this group. Cuticular pustules and microtrichia are often re-

duced, and certain genera (e.g., the *Frankliniella-Taeniothrips-Thrips* complex) lack divergence in their larval stages, indicating close relationships between them.

PHYLOGENY OF THE SERICOTHRIPINI

There appear to be at least three subtribal groups in the tribe Sericothripini (Fig. 5). The Scirtothripina is seemingly the most specialized, and the Sericothripina is the most primitive. The Scirtothripina have reduced body size, reduced body coloration, and reduced setal ornateness, and lack sclerotized body areas, all of which are derived characters. Lack of cuticular pustules and proliferation of cuticular microtrichia may be specializations in this group.

Of the Scirtothripina genera, *Drepanothrips* is here considered the more primitive because most body setae in the members of this genus are terminally funneled, whereas only certain ones are so in *Scirtothrips*. Most body

setae in *Scirtothrips* are short and pointed, and cuticular pustules are totally lacking, these two features considered here to be derived.

The *Scirtothrips* species show a pattern of setal simplification. *S. niveus* has four pairs of setae terminally funneled, and *S. taxodii* and *S. brevipennis* have only two pairs of funneled setae, the latter situation being the derived state.

In the Sericothripina the genus *Sericothrips* contains two subgroups, the *annulipes* and *tiliae* groups. The *tiliae* group is characterized by light body coloration, a lack of hypodermal pigmentation, reduced brown sclerotized areas, and reduced rings at the bases of the setae, all considered here to be derived conditions (Fig. 5). The *annulipes* group is characterized by the presence of cuticular and hypodermal

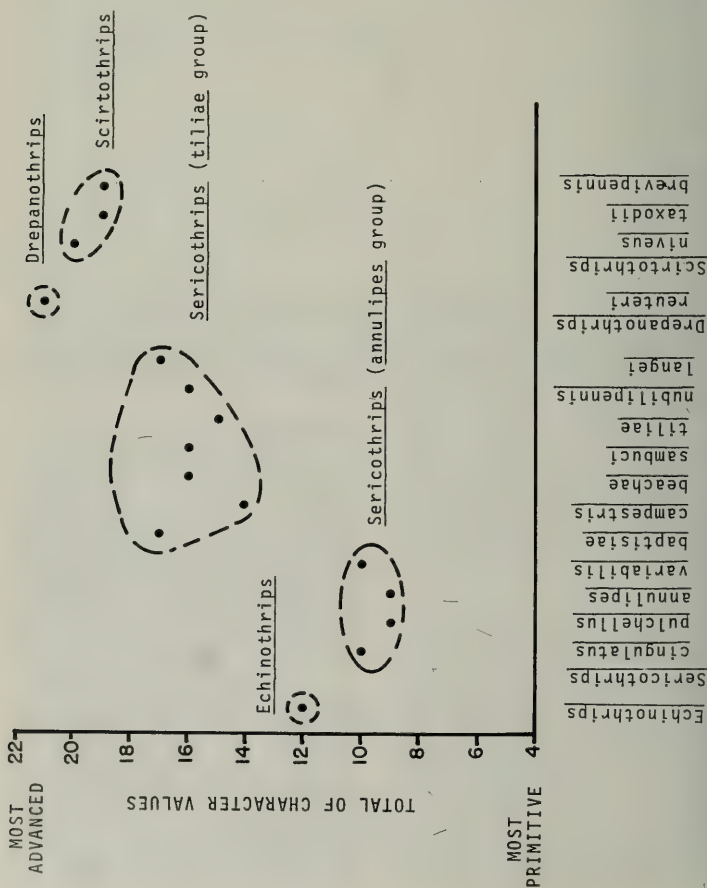


Fig. 4.—Comparison of the degree of derivation among the genera and species of the Sericothripini. These comparisons are based for each group on the total of the values of larval characters shown in Table 4 and totaled in Table 5. The higher a group's total of character values, the more advanced the group is interpreted to be.

pigmentation, brown sclerotized body areas, occasional enlarged rings at the setal bases, and, in one species, by small cuticular pustules, all suggested here to be the primitive state.

The *tiliae* group includes *campestris*, *beachae*, *sambuci*, *tiliae*, *nubilipennis*, *baptisiae*, and *langei* (Fig. 5). The first

five species all have long body setae, and the other two, short setae. *S. campestris* resembles members of the *annulipes* group, having orange cuticular pigmentation and generally long, wide body setae. For these reasons *campestris* is considered the most primitive of the *tiliae* group. *S. beachae*, *S.*

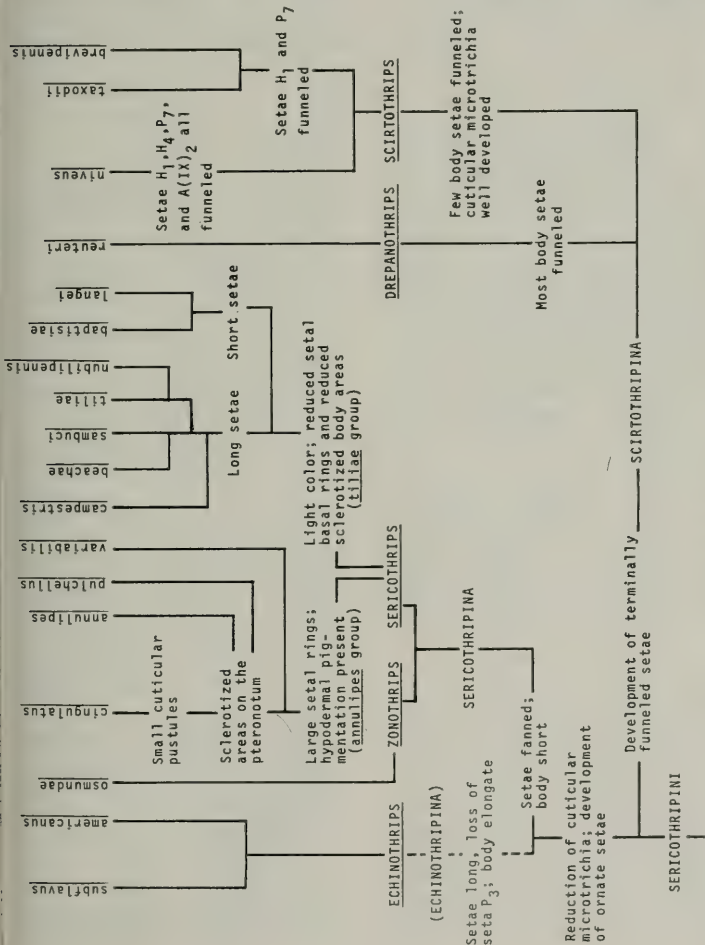


Fig. 5.—Phylogeny of the Sericothripini, based on larval characters. This phylogeny indicates the probable origins of the taxa.

sambuci, *S. tiliae*, and *S. nubilipennis* are light colored and have long setae; *beachae* and *sambuci* have wide setae, and *tiliae* and *nubilipennis* narrow setae. The larvae of the latter two species are seemingly indistinguishable, suggesting that they separated relatively recently. *S. baptisiae* and *langei* are considered to be the most derived of the *tiliae* group because of their setal reduction, those of *langei* being so narrow as to approach the condition found in the Scirtothripina.

The *annulipes* group includes *cingulatus*, *annulipes*, *pulchellus*, and possibly *variabilis* (Fig. 5). The most primitive species is *cingulatus*, as evidenced by its brown body areas, the presence of small cuticular pustules similar to those of the Chirothripini, its pteronotal sclerotized plates, and its enlarged setal basal rings. *S. annulipes* and *pulchellus* have a reduced amount of brown coloration and fewer pustules, but possess pteronotal sclerotized plates, setal basal rings, and hypodermal pigmentation. *S. variabilis* lacks pteronotal sclerotized plates, but has hypodermal pigmentation and somewhat enlarged setal basal rings.

The evolutionary status of the Echinothripina is uncertain. *Echinothrips* species have large body size and ornate setae, both primitive features, but also show derived features, such as weak body coloration and sclerotization and a reduction in certain setae.

SYSTEMATICS

The known larvae of the Thysanoptera of Illinois are described here at the family level and for the suborder Terebrantia at the subfamily and tribal levels. Genera and species larvae are described only for the tribe Sericothripini. Larval descriptions pertain to the second-instar larva unless otherwise stated and include as little repetition as possible from higher to lower groups. A key is included to the major groups and to many genera of the Illinois

thrips fauna, and keys to the species of some genera of the Sericothripini are given.

Measurements, taken with a calibrated ocular micrometer, are expressed in microns. They include lengths and widths of antennal segments, antennal length, body length (excluding antennae), head and pronotal length and width, and lengths of certain body setae, the particular setae measured depending on the genus considered. The setal numbering system used in this report is given in Fig. 6.

KEY TO IMMATURES OF THE THYSANOPTERA

1. Antennae projecting forward, with distinct segmentation; wing pads absent (LARVA) 5
 - Antennae short, projecting back over head or to side of head and indistinctly segmented; if antennae project forward, they are indistinctly segmented 2
2. Antennae directed forward and indistinctly segmented or short and directed laterally or directed posteriorly along sides of head, not reaching anterior margin of prothorax (If antennae are recurved over head, wing pads reach only to second or third abdominal segment.) (PRE-PUPA) 3
 - Antennae are recurved posteriorly over dorsum of head or along sides of head, reaching or surpassing anterior margin of pronotum (PUPA) 4
3. Antennae long and directed forward (recurved over head in *Aeolothrips*); wing pads, if present, extending posteriorly only to second or third abdominal segment; abdominal segment X not tubelike Terebrantia Prepupa
 - Antennae short and directed to side or if long, posteriorly directed along sides of head; wing pads absent; abdominal segment X tubelike or elongately conical. . Tubulifera Prepupa
4. Antennae directed posteriorly over dorsum of head; wing pads, if present, reaching abdominal segment VI or VII; abdominal segment X never tubelike Terebrantia Pupa
 - Antennae directed posteriorly along sides of head; wing pads, if present, reaching to abdominal segment

- II or III; abdominal segment X tubelike or elongately conical
.....**Tubulifera Pupa**
5. Abdominal segment X never tube-like, usually broader than long; middle antennal segments with microtrichia-bearing annulations
.....**Terebrantia Larva**
- Abdominal segment X tubelike or elongately conical, usually longer than wide; middle antennal segments without annulations (Fig. 21, 42, and 61).....**Tubulifera Larva**

GENERIC KEY TO LARVAE
OF THE TEREBRANTIA OF ILLINOIS

1. Prothorax usually with six pairs of setae; abdominal segment IX with three or four pairs of setae...**Larva I**
- Prothorax usually with seven pairs of setae; abdominal segment IX with five or six pairs of setae (**LARVA II**) 2
2. Antennal segment V from one-half to equal to the length of antennal segment IV (**PRIMITIVE FAMILIES**) 3

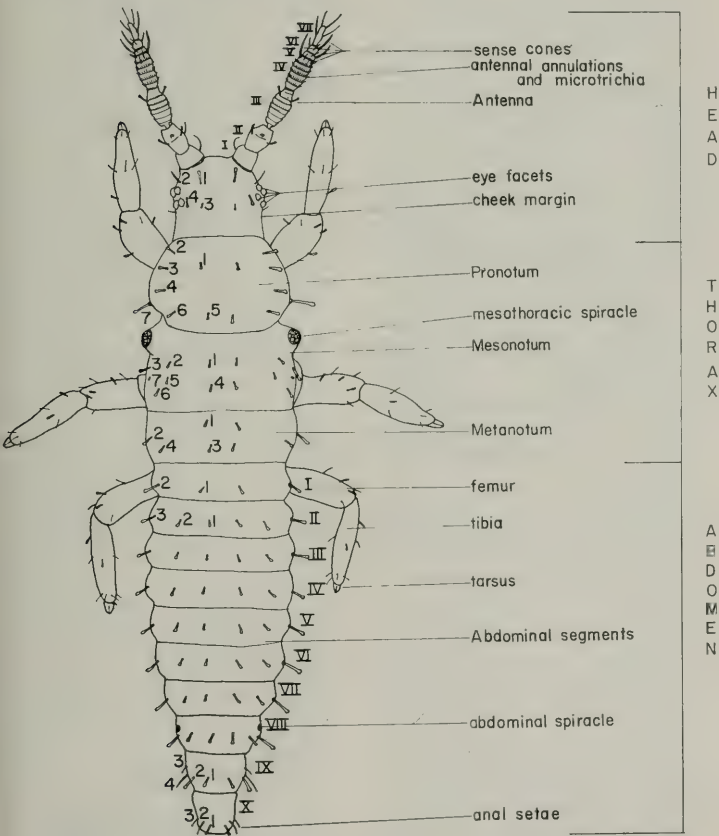


Fig. 6.—The external morphology of a Terebrantian larva (*Sericotrips langei*).

- Antennal segment V much less than one-half the length of segment IV (usually about one-fifth as long) (THRIPIDAE) 6
3. Antennal segment V one-half the length of segment IV (Fig. 22); segments VI and VII with visible annulations **Heterothripidae** (genus *Heterothrips*)
- Antennal segment V equal or subequal to length of segment IV; segments V, VI, and VII with or without annular rings 4
4. Antennal segments VI and VII fused; segments V-VII without annular rings, and segments III and IV not greatly elongated (Fig. 20) **Merothripidae** (genus *Merothrips*)
- Antennal segments VI and VII not fused; segments V-VII with annulations, and segments III and IV elongated (Fig. 18) (AEOLOTHRIPIDAE) 5
5. Four median dorsal setae on abdominal segment IX thornlike (Fig. 57) **Aeolothrips**
- Four posterior setae on abdominal segment IX not thornlike; not yet found in Illinois **Franklinothrips**
6. Antennal segment VII greatly elongated, length seven to eight times the greatest width (Fig. 25) (HELIOTHRIPINAE) 7
- Antennal segment VII not greatly elongated, length only two to three times the greatest width (THRIPINAE) 10
7. Abdominal segment X with six anal setae 8
- Abdominal segment X with less than six anal setae 9
8. Body setae somewhat fanned for entire length (Fig. 46) **Caliothrips**
- Body setae moderately long and simple, with hyaline terminal knob (Fig. 43) **Heliothrips**
9. Body setae moderately long and widely funneled at tip. **Parthenothrips**
- Body setae very short and simple (Fig. 65) **Hercinothrips**
10. Body cuticle generally smooth, with minute pustules or a stippling of fine microtrichia; abdominal segment IX never with a posterior comb (CHIROTHRIPINI, SERICOTHRIPINI, DENDROTHRIPINI) ... 11
- Body cuticle generally with raised protuberances or pustules, with or without microtrichia; with or without a posterior comb on abdominal segment IX (ANAPHOTHRIPINI, THRIPINI) 19
11. All major dorsal body setae expanded and fimbriate or quite long and fimbriate, or if most dorsal body setae are small and simple, cuticle densely covered with fine but obvious (under high-power magnification) microtrichia (SERICOTHRIPINI) 12
- Setae mostly small and simple and cuticle with stippling pattern devoid of obvious microtrichia (DENDROTHRIPINI, CHIROTHRIPINI) 15
12. Setae only terminally funneled, not greatly fimbriate (SCIRTOTHRIPINA) 13
- Setae fanned and fimbriate for most of length (except in *Sericothrips langei*) (SERICOTHRIPINA) 14
- Setae long, unexpanded, and fimbriate for most of length (Fig. 54) (ECHINOTHRIPINA) **Echinothrips**
13. Cuticle with closely set microtrichia; a maximum of four or five pairs of setae expanded, the remainder small and simple (Fig. 49 and 50) **Scirtothrips**
- Cuticle with prominent stippling and with less dense and less obvious microtrichia; all major dorsal body setae terminally funneled (Fig. 52) **Drepanothrips**
14. Associated adults with eight antennal segments; found statewide in Illinois **Sericothrips**
- Associated adults with seven antennal segments; found only in Volo Bog in Lake County, Illinois. . . **Zonothrips**
15. Eye facets large and eyes bulging at sides of head; brown sclerotized body areas lacking (DENDROTHRIPINI) 16
- Eye facets reduced and eyes not bulging at sides of head; brown sclerotized areas present or if absent, antennae and legs greatly reduced (CHIROTHRIPINI) 18
16. Lateral abdominal setae with minute terminal knobs **Leucothrips**
- Certain dorsal body setae terminally funneled 17
17. Lateral setae expanded only on abdominal segment IX (Fig. 71) **Dendrothrips**
- Lateral setae expanded on abdominal segments II-IX and posteroangular

- setae also expanded (Fig. 74) **Pseudodendrothrips**
18. Antennae and legs greatly reduced; all body setae reduced and pointed (Fig. 45) **Chirothrips**
- Antennae and legs not reduced; certain body setae on posterior abdominal segments long and knobbed (Fig. 44) **Limothrips**
19. Cuticular protuberances without microtrichia; abdominal segment IX without posterior comb (except in some *Anaphothrips*); body often with brown sclerotized areas; all or certain setae often knobbed or blunted (ANAPHOTHRIPINI) 20
- Cuticular protuberances with or without microtrichia; abdominal segment IX with a posterior comb (except in *Scolothrips*); body without brown sclerotized areas; setae usually pointed (THRIPINI) 24
20. Median and lateral dorsal setae on abdominal segment IX all nearly equal in length and width 21
- Median setae significantly shorter or thicker than lateral dorsal setae on abdominal segment IX 22
21. Dorsal setae on abdominal segment IX pointed, with prominent rings at bases (Fig. 67) **Anaphothrips**
- Dorsal setae narrowly fanned, without fimbriation and without basal rings **Chaetanaphothrips**
22. Most body setae roundly blunt; mid-dorsal setae of abdominal segment IX shorter and much thicker than lateral setae and almost thornlike (Fig. 66) 23
- All body setae pointed; mid-dorsal setae of abdominal segment IX not thornlike; lateral setae long and whiplike **Aptinothrips**
23. Abdominal tergal sculpture in form of wavy, thickened, raised, transverse striae **Chilothrips**
- Abdominal tergal sculpture in form of raised pustules arranged in transverse rows **Oxythrips**
24. All body setae quite long (each epimeral seta = $60\mu\text{m}$); posterior comb absent on abdominal segment IX (Fig. 56 and 77) **Scolothrips**
- Body setae much shorter, normally less than $30\text{--}40\mu\text{m}$; posterior comb present on abdominal segment IX.. 25
25. Antennal segment IV reduced and shorter than the combined length of segments V-VII (IV about two-thirds the length of V-VII) (Fig. 37) **Ctenothrips**
- Antennal segment IV not reduced and equal to or longer than the combined length of segments V-VII.... 26
26. Other Thripini genera (*Baliothrips*, *Dorcadothrips*, *Frankliniella*, *Iridothrips*, *Microcephalothrips*, *Odonthrips*, *Plesiothrips*, *Rhaphidothrips*, *Taeniothrips*, and *Thrips*) larvae cannot be keyed at this time.

AEOLOTHRIPIDAE Uzel (1895)

Larva.—Antennae (Fig. 8, 18, and 19) each seven segmented; segments III-V elongate, III-VII with well-developed, numerous annular rings; microtrichia present on most annuli. Antennal segment V as long as or longer than IV. Sense cones (segments IV-VI) generally long and pointed.

Head (Fig. 39) usually rounded from the dorsal aspect, with well-developed tentorium, mouth cone short and hypognathous; body elongate and cylindrical. Setae usually long, moderately stout, and pointed or knobbed. Abdominal tergite IX (Fig. 57) with two median pairs of setae modified into stout spines (not modified in *Franklinothrips*). Cuticle with fine microtrichia producing a stippled pattern.

Larva I lacking stout spines on abdominal segment IX.

Diagnosis.—Larvae of the Aeolothripidae are easily distinguished by antennal features: segments III-V are elongate, annular rings are numerous on segments III-VII, and segment V is as long as or longer than segment IV. In heterothripids, antennal segment V is about one-half the length of segment IV, and in the Thripidae, segment V is greatly reduced and less than one-fourth the length of IV.

In the Merothripidae, antennal segment V is as long as IV, but both are relatively short, fewer annulations occur on the antennal segments, and segments VI and VII in *Merothrips* are fused.

Descriptions of *Aeolothrips*, *Melanthrips*, and *Ankothrips* larvae and a key to species of *Aeolothrips* larvae were given by Priesner (1926b-1928). In 1960 Priesner presented a key to the genera of larval Aeolothripidae, includ-

ing *Franklinothrips* and *Rhaphidothrips* in addition to those mentioned above, and gave descriptions of the larvae of *Melanthrips* and *Rhaphidothrips* and some larval characters of *Aeolothrips* and *Franklinothrips*.

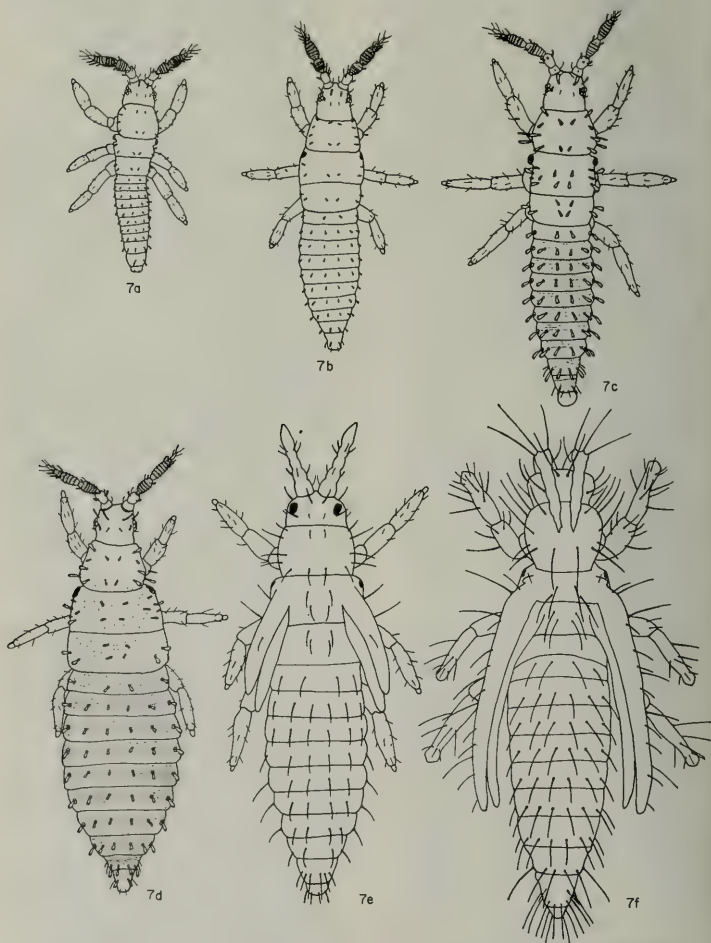


Fig. 7.—Immature stages of *Sericothrips variabilis*. a, Early first-instar larva. b, Late first-instar larva. c, Early second-instar larva. d, Late second-instar larva. e, Prepupa. f, Pupa.

Melis (1959) published descriptions (in Italian) and illustrations of *Aeolothrips* and *Melanthrips* immatures.

Material Examined.—INHS: *Aeolothrips bicolor* Hinds; 1 larva I; June; on grasses; Vermilion County, Illinois.

A. fasciatus (Linneaus); 5 larvae I, 2 larvae II; August and September; on soybeans; Champaign County, Illinois.

A. vittipennis Hood; 3 larvae I, 3 larvae II; June and July; on black locust; Johnson and Union counties, Illinois.

MEROTHRIPIDAE Hood (1914)

Larva.—Antennae (Fig. 20) each six segmented, segments VI and VII usually fused; segments not elongate, having faint annular rings and lacking microtrichia; segment V as long as segment IV.

Head and pronotum (Fig. 40) small and tapering anteriorly, posterior and anterior tentorial arms joined. Body cylindrical. Setae generally long and pointed. Abdominal tergite IX (Fig. 58) with two median pairs of setae modified into stout spines. Cuticle with very fine microtrichia on abdomen and pteronotum, producing a stippled pattern.

Diagnosis.—Merothripid larvae can be easily distinguished by the fusion of antennal segments VI and VII and by the reduction of annular rings and absence of the annular microtrichia found in other families of the Terebrantia.

The larvae of the Merothripidae appear to be transitional between those of the Aeolothripidae and Phlaeothripidae (suborder Tubulifera). Antennal segment V is relatively long in *Merothrips*, as in the Aeolothripidae and Phlaeothripidae, but it is reduced in the Heterothripidae and Thripidae. Merothripids have the median setae of abdominal tergite IX modified into spines, as in the Aeolothripidae, and a reduced number of annular rings and a lack of microtrichia on the antennal segments, as in the Phlaeothripidae.

Material Examined.—INHS: *Merothrips morgani* Hood; larva II, 1 ♂; 28 September 1952; on ground cover; Key West, Florida.

HETEROTHRIPIDAE Bagnall (1912)

Larva.—Antennae (Fig. 9 and 22) each seven segmented, segments II–V with four or five annular rings, segments VI and VII with two or three annular rings; microtrichia present on most rings; segment V about half the length of IV.

Setae short to long and blunt to terminally funneled. Abdominal tergite IX (Fig. 59) with two median pairs of setae modified into stout spines. Cuticle with prominent pustules bearing fine microtrichia (Fig. 41).

Larva I with stout spines on abdominal segment IX.

Diagnosis.—Larvae of the Illinois Heterothripidae can be distinguished by the length of antennal segment V and by a combination of many features which they share with aeolothripid and thripid larvae. Heterothripid larvae appear transitional between Aeolothripidae and Thripidae larvae. Antennal segment V is relatively long, annular rings are present on segments VI and VII, and two pairs of setae on abdominal tergite IX are modified into stout spines, characteristics also present in aeolothripids. The shorter antennal segments with fewer annular rings and the presence of cuticular pustules are thripid characteristics.

Material Examined.—INHS: *Heterothrips arisaemae* Hood; 2 larvae I, 10 larvae II; May–June; on jack-in-the-pulpit (*Arisaema* sp.); La Salle and Carroll counties, Illinois, and Raleigh, North Carolina.

THRIPIDAE Stephens (1829)

Larva.—Antennae each seven segmented, usually only segments III and IV have annular rings (also segments V–VII in the Heliothripinae); micro-

trichia often but not always present on annulations; segment V reduced to less than one-fourth the length of segment IV.

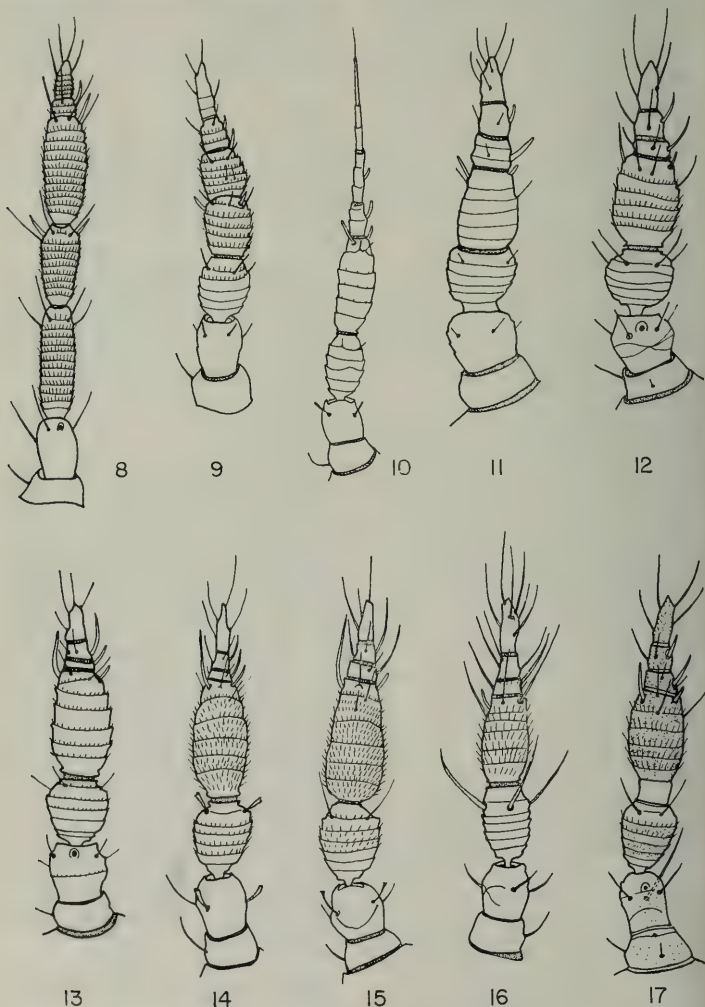


Fig. 8-17.—Right antenna (except where indicated) of the first-instar larva. 8.—*Aeolothrips vittipennis*. 9.—*Heterothrips arisaemae*. 10.—*Heliothrips haemorrhoidalis*. 11.—*Limothrips denticornis*. 12.—*Anaphothrips secticornis*. 13.—*Dendrothrips ornatus*. 14.—*Sericothrips variabilis*. 15.—*Scirtothrips taxodii*. 16.—*Echinothrips americanus*, left antenna. 17.—*Frankliniella tritici*.

Abdominal tergite IX without spines (a posterior comb usually present on tergite IX in the Thripini). Setal features and cuticular sculpturing variable.

Diagnosis.—Larvae of the Thripidae can be recognized by the great reduction of antennal segment V and by the lack of spines on abdominal tergite IX.

The Thripidae include the subfamilies Heliothripinae and Thripinae. These subfamilies and their tribes are distinguished by antennal features, cuticular sculpturing, and other characteristics.

Subfamily HELIOTHRIPINAE

Karny (1921)

Larva.—Terminal antennal segment greatly elongate (length seven to eight times the greatest width, as in Fig. 10, 25, 26, and 27); antennae with annulations on segments V–VII, annulations often with no or few microtrichia; sense cones fairly short. Body often with prominent areas of brown coloration. Cuticle usually with small to large pustules, which generally lack microtrichia. Head usually constricted behind the eyes (Fig. 43 and 46). Abdominal segment IX (Fig. 60, 63, and 65) lacks a posterior comb; segment X sometimes with long anal setae. Body setae variable, often ornate.

Diagnosis.—Larvae of the Heliothripinae are easily recognized by the elongate terminal antennal segments and by the combination of features mentioned above. The Heliothripinae may be considered the most primitive subfamily in the Thripidae. Primitive features are the elongate antennal segments, the presence of annulations on the terminal segments, and the shorter sense cones found also in the Aeolothripidae. The Heliothripinae resemble the Anaphothripini in having cuticular pustulation, cheek constrictions, and body areas of brown sclerotization. They resemble the Chirothripini in

having a reduced number of annular microtrichia, an enlarged antennal segment V (in the first-stage larva of *Limothrips*), and body areas of brown sclerotization.

The only native genus of this subfamily in Illinois is *Caliothrips*; exotic genera occurring in greenhouses and homes are *Heliothrips*, *Parthenothrips*, and *Hercinothrips*.

Material Examined.—INHS: *Caliothrips indicus* (Bagnall); 2 larvae I, 1 larva II; 3 March 1970; reared from soybeans; Jabalpur, M.P., India.

Heliothrips haemorrhoidalis var. *angustior* Priesner; 1 larva I, 3 larvae II, prepupa (on slide with ♀ lectotype); on plants of virgin forest; Paramaribo, Surinam, S.A.

Hercinothrips femoralis (Reuter); 1 larva II; 30 April 1953; on African violet; St. Louis, Missouri.

Parthenothrips dracaenae (Heeger); 1 larva II; March 1952; on *Cordyline feminalis* leaves; Wahiawa, Oahu, Hawaii.

Subfamily THRIPINAE

Stephens (1829)

Larva.—Terminal antennal segments not greatly elongated (length only two to three times the greatest width), antennae without annulations on segments V–VII, antennal microtrichia and sense cones variable. Body coloration, cuticular sculpturing, head shape, and abdominal segment IX variable. Abdominal segment X lacks long anal setae.

Diagnosis.—Larvae of the subfamily Thripinae can be distinguished from those of the Heliothripinae by the short, terminal antennal segments and by other features not usually occurring in the Heliothripinae.

Priesner (1957) recognized the tribes Dendrothripini, Sericothripini, Thripini, and Chirothripini in the Thripinae, and included the Anaphothripini under the Thripini as a subtribe. Stannard (1968) recognized these tribes, too, but tenta-

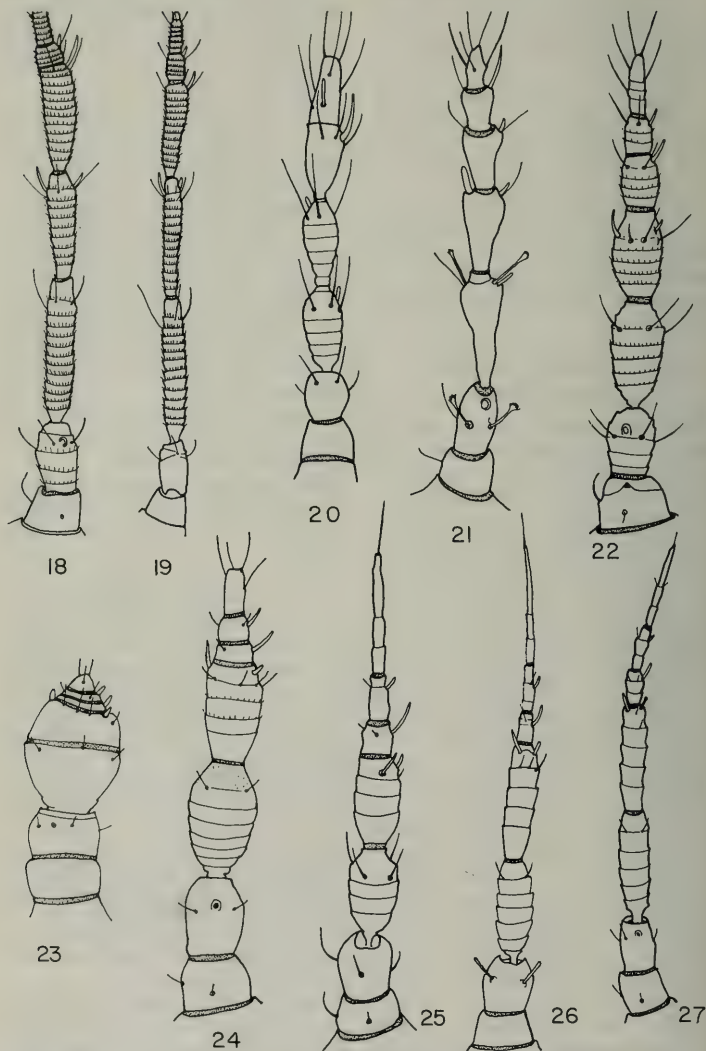


Fig. 18-27.—Right antenna of the second-instar larva. 18.—*Aeolothrips vittipennis*. 19.—*Franklinothrips* sp. 20.—*Merothrips morgani*. 21.—Phlaeothripid (*Tubulifera*). 22.—*Heterothrips arisaemae*. 23.—*Chirothrips simplex*. 24.—*Limothrips cerealium*. 25.—*Caliothrips indicus*. 26.—*Heliothrips haemorrhoidalis*. 27.—*Hercinothrips femoralis*.

tively included the Chirothripini under the Thripini because of difficulties in their categorization.

Here, five tribes are tentatively recognized in the Thripinae: the Chirothripini, Anaphothripini, Dendrothripini, Thripini, and Sericothripini. Certain combinations of larval features have been found to be characteristic of each tribe. Important characters at the tribal level include cuticular sculpturing; features of the antennal annulations, microtrichia, and sense cones; presence or absence of a posterior comb on abdominal tergite IX; and to a lesser extent the setal types and brown sclerotized body areas.

Tribe CHIROTHIRPINI Priesner (1949)

The diagnostic features of Chirothripine larvae are: (1) cuticle with small pustules bearing minute microtrichia, (2) body setae simple with certain ones knobbed (Fig. 64) (all reduced and pointed in *Chirothrips*) (Fig. 45 and 62), (3) head and pronotum often with brown sclerotized areas (Fig. 44) (reduced in *Chirothrips*) (Fig. 45), (4) antennal microtrichia greatly reduced, (5) antennal sense cones short to moderately long (Fig. 23 and 24), and (6) eye facets small and not bulging at sides of head.

The Chirothripini larvae resemble the Heliothripinae larvae in the reduction of the annular microtrichia on the antennae, segment V in the first-stage larva being longer and having two annulations (Fig. 11) (a trait found in most Heliothripinae but in no other Thripinae). The brown sclerotized areas of *Limothrips* resemble those found in many Heliothripinae.

Two genera in this tribe occur in Illinois, *Chirothrips* and *Limothrips*. Both contain species that are grain feeders and can be serious pests.

Material Examined.—INHS: *Limothrips cerealium* (Haliday); 1 larva II; 24 June 1953; Kenney, Illinois.

USNM: *Chirothrips simplex* Hood; 10 larvae II, 1 prepupa; 21 October 1961; reared from *Bouteloua eriopoda*; Las Cruces, New Mexico.

Limothrips denticornis Haliday; 2 larvae I, 3 larvae II, 2 prepupae; 10 July 1959; on barley; Northwood, North Dakota.

Tribe ANAPHOTHIRPINI Priesner (1949)

The diagnostic features of anaphothripine larvae are: (1) cuticle covered with large pustules and usually lacking microtrichia; (2) dorsal body setae pointed, knobbed, or blunt; (3) brown sclerotized body areas present in some species (Fig. 47 and 48); (4) posterior comb on abdominal tergite IX usually lacking (Fig. 66 and 67) (sometimes present in *Anaphothrips*); (5) annular microtrichia on antennae generally reduced (Fig. 12, 28, and 29); and (6) antennal sense cones moderately long to long.

The status of the Anaphothripini has long been variously interpreted. Priesner (1957) included the members of this tribe within the Thripini. Gentile & Bailey (1968) considered the Anaphothripini to be the most primitive of all thripine tribes, and Stannard (personal communication) is of the opinion that the Anaphothripini are close to the Heliothripinae.

The larvae of the Anaphothripini resemble those of the Heliothripinae in cuticular sculpturing, the presence of brown coloration in some species, a reduction of antennal microtrichia, and other features. They resemble the Thripini larvae in cuticular sculpturing and in the posterior comb that is sometimes present in *Anaphothrips*. *Anaphothrips secticornis* has brown sclerotized areas on the pteronotum similar to those in the *annulipes* group of *Sericothrips*. *Chaetanaphothrips* possesses expanded setae similar to those of *Sericothrips*.

In Illinois the tribe Anaphothripini

is represented by *Anaphothrips*, *Aptinothrips*, *Bregmatothrips*, *Chaetanaphothrips*, *Chilothrips*, *Oxythrips*, and *Prosopothrips*.

Material Examined.—INHS: *Anaphothrips secticornis* Karny; 3 larvae I, 6 larvae II; 21 January 1964; on short grasses; Barff Peninsula, Sörling Valley, South Georgia Island.

Aptinothrips rufus (Gmelin); 8 larvae I, 4 larvae II; 23 June 1933; on timothy heads; Champaign County, Illinois.

Oxythrips cannabensis Knechtel; 13 larvae I, 20 larvae II; August; on marijuana; Henry and Morgan counties, Illinois.

Chilothrips pini Hood; 5 larvae II; on cottonwood; 15 October 1959; Parkland, Adams County, Wisconsin.

Chilothrips sp.; 4 larvae II; on rotten wood and pigmy cypress duff; Deschutes County, Oregon, and Mendocino County, California.

Tribe DENDROTHRIPINI Priesner (1926b-1928)

The diagnostic features of dendrothripine larvae are: (1) cuticle covered with minute microtrichia, resulting in a stippled pattern and forming larger pustules in transverse rows on the terminal abdominal segments (Fig. 71); (2) body setae generally simple but with certain ones terminally knobbed (Fig. 74); (3) brown sclerotized areas lacking (Fig. 51); (4) antennal sense cones long (Fig. 35 and 36); (5) antennal microtrichia prominent and located between the annulations on segment IV (larva I) (Fig. 13), as in the Sericothripini.

Larval characters of the Dendrothripini are well defined and easily delineated; the larvae are very similar to those of the Sericothripini. Cuticular sculpturing is similar to that of the Sericothripina, and setae are similar to those of the Scirtothripina. Random microtrichia on antennal segment IV

are also diagnostic for larvae of the Dendrothripini and Sericothripini.

The tribe Dendrothripini in Illinois includes one native genus, *Leucothrips*, and two genera introduced from Europe and Japan, *Dendrothrips* and *Pseudodendrothrips*, respectively.

Material Examined.—INHS: *Dendrothrips ornatus* (Jablonowski); 5 larvae I, 3 larvae II; 23 August 1955; on privet; Champaign County, Illinois.

Leucothrips piercei (Morgan); 1 larva I, 3 larvae II; 20 June 1967; on redbud leaves; Montgomery County, Illinois.

Pseudodendrothrips mori (Niwa); 1 larva I, 4 larvae II; 25 October 1961; on Japanese mulberry leaves; McLean County, Illinois.

Tribe THRIPINI Stephens (1829)

The diagnostic features of thripine larvae are: (1) cuticle covered with small to large pustules (Fig. 55), often with microtrichia present; (2) dorsal body setae pointed (Fig. 56), knobbed, blunt, or terminally funneled; (3) brown sclerotized body areas usually absent; (4) posterior comb or teeth usually present on abdominal tergite IX except in *Scolothrips* (Fig. 75, 76, and 77); (5) antennal annular microtrichia not reduced; and (6) antennal sense cones short to moderately long (Fig. 17, 37, and 38).

The Thripini larvae resemble the Anaphothripini larvae in cuticular sculpturing and general body appearance. Generally, less diversification is found among closely related members of the Thripini than is usual among the members of other tribes.

The tribe Thripini in Illinois includes *Baliothrips*, *Ctenothrips*, *Dorcadothrips*, *Frankliniella*, *Iridothrips*, *Microcephalothrips*, *Odonotothrips*, *Plesiothrips*, *Rhaphidothrips*, *Scolothrips*, *Taeniothrips*, and *Thrips*.

Material Examined.—INHS: *Ctenothrips bridwelli* Franklin; 1 larva II; 11

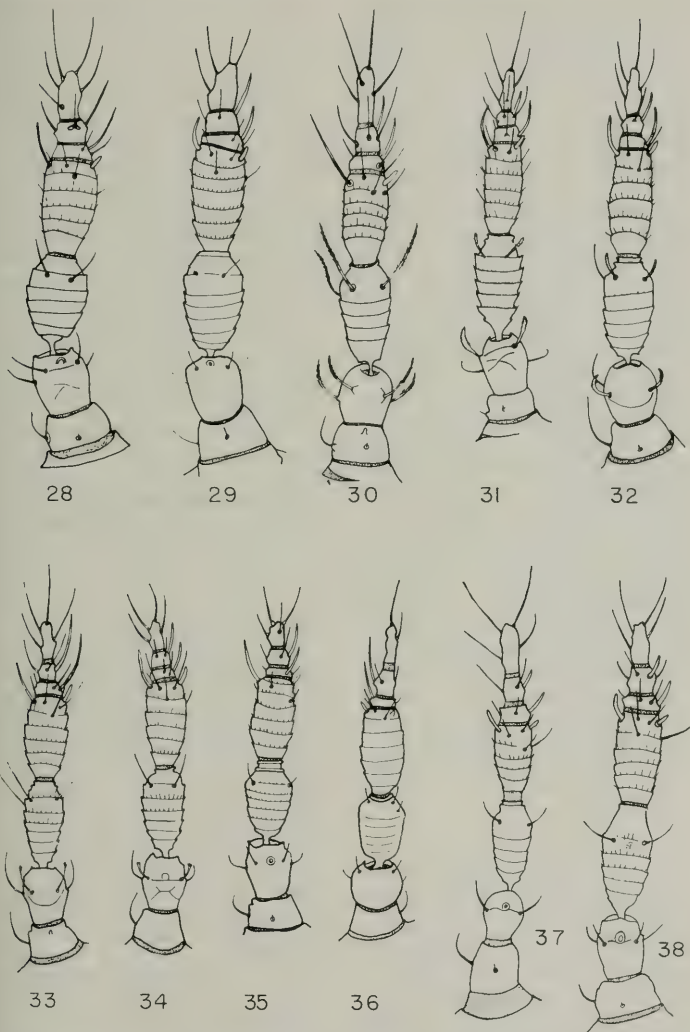


Fig. 28-38.—Right antenna (except where indicated) of the second-instar larva. 28.—*Anaphothrips septicornis*. 29.—*Oxythrips cannabensis*. 30.—*Echinothrips americanus*. 31.—*Sericothrips annulipes*. 32.—*Sericothrips variabilis*. 33.—*Scirtothrips taxodii*. 34.—*Drepanothrips reuteri*. 35.—*Dendrothrips ornatus*. 36.—*Pseudodendrothrips mori*, left antenna. 37.—*Ctenothrips bridwelli*. 38.—*Taeniothrips simplex*.

July 1947; on *Arisaema dracontium*; La Salle County, Illinois.

Frankliniella fusca (Hinds); 3 larvae II; 9 June 1949; Berlese collecting method; Mercer County, Illinois.

F. parvula Hood; 1 larva II; 20 June 1970; on bananas; Ciudad Chontalpa, Tabasco, Mexico.

F. tritici (Fitch); 1 larva I, 9 larvae II; on flowers of yarrow and Culver's root flowers; Lake, Livingston, and Massac counties, Illinois.

Frankliniella sp.; 12 larvae II, 3 prepupae, 2 pupae; May-July; on oats and from Berlese collecting method; Jackson County, Illinois, and Friday Harbor, Washington.

Microcephalothrips sp.; 5 larvae II; 16 December 1949; on Spanish moss; Chiefland, Florida.

Scolothrips pallidus (Beach); 1 larva II; 28 July 1964; on cotton; Kewanee, Missouri.

Taeniothrips simplex (Morison); 10 larvae II, 7 prepupae, 11 pupae; July-August; on gladiolus; Champaign and Will counties, Illinois.

Thrips impar Hood; 1 larva I, 5 larvae II; 16 July 1969; on jewelweed; Edward, Henry, and McLean counties, Illinois.

Thrips physapus Linneaus; 1 larva II; December 1959; Recoaro, Italy.

Thrips tabaci Lindeman; 1 larva I, 1 larva II; 25 April 1968; on clover; Champaign County, Illinois.

Tribe SERICOTHRIPINI Priesner (1926b-1928)

The diagnostic features of sericothripine larvae are: (1) cuticle covered with fine microtrichia, resulting in a stippled pattern over the abdomen and pteronotum; (2) cuticular pustules absent or very reduced; (3) all or some dorsal body setae expanded and/or fimbriate; (4) brown sclerotization lacking; (5) fourth antennal segment of first-instar larva densely covered with microtrichia.

The tribe Sericothripini is divided into the subtribes Sericothripina, Scirtothripina, and a new subtribe, the Echinothripina. Each of these groups is distinctive in certain larval characteristics, and each shows certain similarities with other tribes, indicating possible lines of relationship.

Sericothrips, particularly the *annulipes* group, resembles the Anaphothripini in such genera as *Anaphothrips* and *Chaetanaphothrips*. Most members of the *annulipes* group possess pteronotal sclerotized areas similar to those found in *Anaphothrips secticornis*. *Sericothrips cingulatus* has darker brown markings and small pustules reminiscent of those in the Anaphothripini and Chirothripini. *Chaetanaphothrips* has fanned (but not fimbriate) setae similar to those in *Sericothrips*.

Scirtothrips and *Drepanothrips* show similarities to the Dendrothripini in setal features, coloration, and cuticular sculpturing.

Subtribe SERICOTHRIPINA Priesner (1957)

Larvae of the Sericothripina are characterized by fan-shaped, fimbriate setae; minute cuticular microtrichia set on pustulelike bases on the terminal abdominal segments; and the absence of pustules elsewhere. An exception is *Sericothrips cingulatus*, in which all microtrichia are set on small pustules. Microtrichia in all *Sericothrips* species form transverse rows on the abdomen, especially on the terminal abdominal segments, similar to the rowed ordering of the larger pustules in other groups.

Setal form in this group is unique among all thrips larvae and is an easily recognized diagnostic character. *Caliothrips* and possibly *Chaetanaphothrips* have fan-shaped setae somewhat like those of the Sericothripina, but the setae of *Caliothrips* and *Chaetanaphothrips* are smooth rather than fimbriate. The only genera in the Sericothripina

in Illinois are *Sericothrips* Haliday and *Zonothrips* Priesner.

Subtribe SCIRTOTHRIPINA
Priesner (1957)

Larvae of the Scirtothripina are characterized by setae expanded or funneled terminally only and by long, dense cuticular microtrichia in the absence of cuticular pustules. Larvae of this subtribe are smaller than those of the Sericothripina and tend to have less ornamentation and less interspecific variation. Larval Scirtothripina have no hypodermal pigmentation, brown sclerotized areas, or setal basal rings; the setae are much simpler, and no cuticular pustulation is evident except for transverse rows formed by stippling on abdominal segments IX and X. Scirtothripina larvae resemble those of the Dendrothripini in their setae, both having combinations of long, terminally-funneled and short, pointed setae. Larvae of the Scirtothripina can be easily identified (particularly *Scirtothrips*) by their dense, long cuticular microtrichia and their lack of cuticular pustules. The genera included in this subtribe, according to Priesner (1957), are *Charassothrips* Hood, *Drepanothrips* Uzel, *Enneothrips* Hood, *Ensiferothrips* Bianche, *Octothrips* Moulton, *Scirtodothrips* Hood, *Scirtothrips* Shull, and *Sericopsothrips* Hood.

Subtribe ECHINOTHRIPINA,
New Subtribe

The proper placement of the genus *Echinothrips* in higher categories has long been in question. Moulton (1911) placed *Echinothrips* in the Heliothripinae, and Medina as late as 1961 still considered this to be the best placement. Priesner (1957), however, considered this genus to be in the Thripini because of imaginal endothoracic morphology, and Stannard (1968) transferred *Echinothrips* into

the Sericothripini because of the presence of abdominal microtrichia and the lack of fusion of the fore vein to the costa in the fore wing of the adults.

The larval characters of *Echinothrips* support Stannard's placement of the genus. Similarities of *Echinothrips* larvae to the larvae of other Sericothripini genera can be seen in cuticular microtrichia, fimbriate setae, antennal shape and sense cones, and extra microtrichia on antennal segment IV of first-stage larvae. *Echinothrips* differs in its unexpanded and more elongate body setae, larger and more elongate body size, positioning of head setae H1, and loss of pronotal setae P3.

Generally, *Echinothrips* most closely resembles the Sericothripina, but because of the differences described, the genus has been placed in its own subtribe. Wilson (1971) delimits a group of closely related genera that he calls the *Echinothrips* complex, including *Cercyothrips* Morgan, *Echinothrips* Moulton, *Enneothrips* Hood, *Plesiopsothrips* Hood, *Plesiothrips* Hood, and *Pteridothrips* Priesner. Some of these he placed with the Thripini and others with the Sericothripini; Wilson feels that this group is transitional between the Sericothripini and the Thripini and that possibly it merits tribal status. The only genus included here in this subtribe is *Echinothrips* Moulton.

Drepanothrips Uzel (1895)

Larva II.—Body color yellow. Antennal segments, tibiae, bases of femora, setae, and setal basal rings light brown to brown. Apices of antennal segments I and II and base and apex of segment III pale gray. Eyes red.

Antennae each seven segmented (Fig. 34); longer sense cone on segment IV, and sense cones on segments V and VI moderately long and slightly blunted; all of equal length. Segment II with a pair of terminally funneled setae; segment III with six annulations,

the distal three with short microtrichia; segment IV with five annulations, all with longer microtrichia.

Head (Fig. 52) longer than wide. Eyes with four large facets bulging at sides of head. Mouth cone moderately blunt. Head with four pairs of dorsal setae; H1, H3, and H4 subequal and terminally funneled.

Pronotum longer than wide with seven pairs of terminally funneled setae; P6 and P7 somewhat longer than P1-P5. Mesonotum with seven pairs and metanotum with five pairs of funneled setae, all of nearly equal length. Abdominal tergite I with two pairs and tergites II-VIII each with three pairs of funneled setae; A1, A2, and sometimes A3 on tergite IX (Fig. 70) funneled, and all subequal to equal in length. Abdominal tergite X with three pairs of setae, A1 funneled.

Almost all dorsal body setae terminally funneled and of moderate length. Bases of setae with faint brown rings. Abdominal and pteronotal cuticle with dense stippling and fine microtrichia, which are shorter and less obvious than those on *Scirtothrips* and longer than those on *Sericothrips*, stippling forming transverse rows on abdominal segments IX and X. Segment IX lacking a posterior comb.

Diagnosis.—*Drepanothrips* larvae most closely resemble *Scirtothrips* larvae from which they can be distinguished by the dorsal body setae, all of which are terminally funneled, while only a few characteristic ones are funneled in *Scirtothrips*. The cuticular microsetae are shorter and less dense in *Drepanothrips* than they are in *Scirtothrips*. Larvae of *Drepanothrips* differ from those of other *Sericothripini* in having terminally expanded setae, the setae of the other genera being either totally expanded or long and unexpanded. *Dendrothrips* and *Pseudodendrothrips*, which resemble *Drepanothrips* in the larval stages, can be differentiated by their lack of cuticular

microtrichia and by their having only certain dorsal body setae funneled.

The genus contains only one species, *D. reuteri*, in Illinois.

Drepanothrips reuteri Uzel (1895)

(Fig. 34, 52, and 70)

Larva II.—Body light yellow to yellow. Antennae, tibiae, bases of femora, and setal basal rings light brown; antennal segments II, V-VIII, and apex of IV often darker brown. Apices of antennal segments I and II and base and apex of segment III very pale gray. Eyes dark red.

Most body setae slender, terminally funneled or dilated, and subequal in length (14-19 μ m). Bases of setae with faint unraised brown rings. Dorsal sclerotized areas lacking. Stippling forming transverse rows only on abdominal segments IX and X.

Measurements of the *D. reuteri* larva II are shown in Table 6.

Diagnosis.—*D. reuteri* occurs on grapevines (*Vitis* sp.), of which it

Table 6.—Measurements, in microns, of three *Drepanothrips reuteri* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
I	19 ^a	...	22-23
II	28-31	...	22-23
III	42-46	...	22
IV	42-46	...	17-20
V	8-11	...	12-14
VI	8-9	...	9
VII —	16	...	6
Antenna	163-178	171	...
Head	70-78	...	78-85
Pronotum	93-124	...	124-140
Body	660-825	765	...
Setae			
H1	16		
H4	16-19		
P7	16-19		
A(IX)1	14-16		
A(IX)2	17-19		
Ventral setae (IX)	15		

^a A single measurement in a range column indicates that all such measurements were identical.

has been reported to be a pest. Bailey (1942) gave an account of the biology of this thrips and discussed the litera-

ture concerning it. This species has been recorded only once in Illinois, two adult females having been taken in



Fig. 39-48.—Head and pronotum (except where indicated) of the second-instar larva. 39.—*Aelothrips vittipennis*. 40.—*Merothrips morgani*. 41.—*Heterothrips arisaemae*. 42.—*Phlaeothripid (Tubulifera)*. 43.—*Heliothrips haemorrhoidalis*. 44.—*Limothrips cerealium*, head, pronotum, and left foreleg. 45.—*Chirothrips simplex*, head, pronotum, and left foreleg. 46.—*Caliothrips indicus*. 47.—*Oxythrips cannabensis*. 48.—*Anaphothrips secticornis*.

Urbana from a sparrow nest built in a grape arbor.

Material Examined.—INHS: 3 larvae II; 23 August 1965; on grape; collected by K. Stahlik; Selma, Fresno County, California.

Echinothrips Moulton (1911)

Larva II.—Cuticular color usually yellow to orange. Antennal segments, tibiae, bases of femora, and setae generally light brown. Eyes red.

Antennae each seven segmented (Fig. 30); longest sense cone on segment IV, sense cones on V and VI long and pointed; segments II and III each with two pairs of fimbriate setae; segment III with five annulations, none with microtrichia; segment IV with five annulations, all with microtrichia.

Head (Fig. 54) wider than long. Eyes with four large facets bulging at sides of head. Mouth cone moderately blunt. Head with four pairs of dorsal setae, all long and fimbriate; H1 located more posteriorly than usual in most known thrips larvae and almost opposite to H4; H3 and H4 equal and shorter than H1.

Pronotum (Fig. 54) wider than long with six pairs of fimbriate setae; P3 lacking; P1, 2, 4, and 6 all longer than P7. Mesonotum with seven pairs and metanotum with four pairs of long fimbriate setae of varying lengths. Setae A1 and 2 of abdominal segment IX long; A3 of varying length, sometimes reduced (Fig. 73). Segment X with three pairs of dorsal setae; A1 and A3 long and fimbriate.

Most dorsal body setae fimbriate and long, the setal lengths on abdominal tergites sometimes varying greatly. Cuticle with minute microtrichia sparsely scattered on abdominal tergites, microtrichia becoming pustulelike and forming transverse rows on the terminal abdominal segments. Abdominal segment IX lacking a posterior comb.

Larva I.—Cuticle yellow to orange; hypodermal pigment lacking. Antennal segments I, III, and most of IV, tibiae, and bases of femora generally light brown; segment II, apex of IV, and all of V–VII darker brown. Eyes red.

Antennae each seven segmented; suture between IV and V usually distinct. Sense cones on segments IV–VI as in larva II, but longer (Fig. 16). Segments II and III each with a pair of long fimbriate setae. Segment III with five annulations, with minute microtrichia present ventrally. Segment IV with six annulations; microtrichia present randomly on and between annulations but less dense than in *Scirtothrips*. Apical segment not narrowed terminally.

Chaetotaxy similar to that of larva II, except posteroangular setae (P7) lacking, the mesonotum with four pairs of setae, the metanotum with three pairs of setae, and abdominal segment IX with two pairs of dorsal setae. Integument with stippling, as in larva II, but fainter.

Diagnosis.—*Echinothrips* larvae can be easily recognized by their long fimbriate setae and elongate body shape, which are unique among the Thripinae in Illinois. Antennal and cuticular sculpturing are similar to those of *Sericothrips*, but setal length and type, body shape, placement of setae H1 (more posterior in *Echinothrips*), and loss of one pronotal setal pair (P3) differ from those of *Sericothrips*. These features distinguish *Echinothrips* from all other genera. The only other thripine genus in Illinois possessing long setae similar to those in *Echinothrips* is *Scolothrips*.

Interspecific variation in *Echinothrips* is very limited in the two species considered, *E. americanus* and *E. subflavus*. In the one slide of *E. subflavus* studied, body dimensions and setal lengths were larger than those in

E. americanus. However, considerable variation in setal lengths was found in *americanus*; so the extent of variation in both species will have to be investigated before setal measurements can be used as a diagnostic feature.

***Echinothrips americanus*
Morgan (1913)**

(Fig. 16, 30, 54, and 73)

Larva II.—Cuticle yellow to orange. Antennae, tibiae, bases of femora, and



Fig. 49-56.—Head and pronotum of the second-instar larva. 49.—*Scirtothrips niveus*. 50.—*Scirtothrips taxodii*. 51.—*Dendrothrips ornatus*. 52.—*Drepanothrips reuteri*. 53.—*Sericothrips annulipes*. 54.—*Echinothrips americanus*. 55.—*Taeniothrips simplex*. 56.—*Scolothrips pallidus*.

setae brown; apices of antennal segments I and II and base and apex of III light brown. Eyes red.

Most dorsal setae long (50–70 μm) and fimbriate for most of their length; others (H2; Ms1, 2, 5, and 6; and Mt1) shorter (20–30 μm). Light brown spot present on head anteriorly. Cuticle with large stippling on abdomen forming transverse rows and becoming finer and randomly distributed on pteronotum and posterior portion of pronotum.

Measurements of the *E. americanus* larva II are shown in Table 7.

Table 7.—Measurements, in microns, of five *Echinothrips americanus* larvae II.

Character	Length		Range Width
	Range	Mean	
Antennal segment			
I	19–23	...	28–31
II	28–36	...	25–29
III	50–62	...	23–28
IV	43–54	...	19–23
V	11–12	...	16–19
VI	12–16	...	12–16
VII	26–28	...	8 ^a
Antenna	195–217	209	...
Head	85–93	...	96–116
Pronotum	105–124	...	148–178
Body	1,065–1,281	1,167	...
Setae			
H1	54		
H4	39–46		
P7	39–46		
A(IX)1	54–70		
A(IX)2	67–78		
A(IX)3	51–54		
A(X)1	54–67		

^a A single measurement in a range column indicates that all such measurements were identical.

Larva I.—Cuticle yellow to orange. Antennal segments I, III, and most of IV brown; apices of I and II and base and apex of III pale brown; segments II, apex of IV, and V–VII darker brown. Tibiae, bases of femora, and setae light brown. Eyes red.

Setae long and fimbriate as in larva II, but generally shorter (30–45 μm in larva I).

Cuticle with stippling visible only on abdominal segment X.

Measurements of the *E. americanus* larva I are shown in Table 8.

Table 8.—Measurements, in microns, of two *Echinothrips americanus* larvae I.

Character	Length Range	Width Range
Antennal segment		
I	16–19	23–26
II	26–28	23 ^a
III	39–40	23
IV	43–46	23
V	6–8	12
VI	12–16	9
VII	26	8
Antenna	168–183	...
Head	70	88
Pronotum	85	116
Body	807–814	...
Setae		
H1	32–40	
A(IX)1	50–51	
A(IX)2	40–43	
A(X)1	132	

^a A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—*E. americanus* larvae cannot at this time be distinguished from those of *subflavus* except by associated adults and host-plant data and by their somewhat smaller size. *E. americanus* is found on many forest plants, in particular on jewelweed (*Impatiens*).

Material Examined.—INHS: 2 larvae I, 10 larvae II; June–October; on *Desmodium*, hydrangea, and jewelweed foliage; Gallatin, Clark, Henry, and Johnson counties, Illinois.

Echinothrips subflavus Hood (1927b)

Larva II.—Cuticle yellow. Antennal segments, tibiae, bases of femora, and setae brown; apices of antennal segments I and II and base and apex of III light brown. Eyes dark red.

Most dorsal setae long (60–80 μm) and fimbriate for most of their length; others (H2; P7; Ms1, 2, 5, and 6; and Mt1) shorter (25–40 μm). Cuticle with larger stippling on abdomen, and

forming transverse rows and becoming finer and randomly distributed on pteronotum and posterior portion of pronotum.

Measurements of the *E. subflavus* larva II are shown in Table 9.

Table 9.—Measurements, in microns, of one *Echinotrips subflavus* larva II.

Character	Length	Width
Antennal segment		
I	23	31
II	42	28
III	65	25
IV	57	23
V	11	16
VI	16	12
VII	28	8
Antenna	242	...
Head	116	124
Pronotum	124	194
Body	1,350	...
Setae		
H1	62	
H4	46	
P7	28	
A(IX)1	85	
A(IX)2	85	
A(IX)3	60	
A(X)1	85	

Diagnosis.—*E. subflavus* larvae cannot at this time be distinguished from those of *E. americanus* except by associated adults and host-plant data. *E. subflavus* is found on hemlock (*Tsuga canadensis* (L.)) in the eastern United States and could possibly be brought into Illinois on hemlocks intended for ornamental plantings.

Material Examined.—USNM: 1 larva II; 23 July 1939; on hemlock; collected by J. D. Hood; Oswegatchie, New York.

Scirtothrips Shull (1909)

Larva II.—Cuticular color yellow to orange, sometimes with orange hypodermal subintegumental pigment. Antennae, bases of femora and entire tibiae, and an anterior median cephalic spot all light brown to brown. Apices of antennal segments I and II and base and apex of III pale gray.

Antennae each seven segmented (Fig. 33). Longest sense cone on segment IV and sense cones on segments V and VI long, pointed, and all subequal. Segment II with a pair of funneled setae. Segment III with six annulations, fine microtrichia present on all annulations.

Head (Fig. 49) wider than long. Eyes with four large facets bulging at sides of head. Mouth cone moderately blunt. Head with four pairs of dorsal setae; H1 usually and H4 sometimes funneled; H1 and H4 of equal length; H3 subequal to H1 and H4.

Pronotum (Fig. 49) wider than long with seven pairs of dorsal setae. All except the posteroangular setae (P7) short and pointed; P7 longer and often funneled. Mesonotum with seven pairs and metanotum with four pairs of short, pointed dorsal setae. Abdominal segment I with two pairs and segments II–VIII each with three pairs of dorsal setae. Segment IX (Fig. 72) with four pairs of dorsal and lateral setae; A2 longest and sometimes funneled; ventral setae about as long as A1. Segment X with two pairs of dorsal setae; A1 sometimes funneled.

Most setae pointed and fairly short; H1 and P7 always, and H4, A(IX)2, and A(X)1 sometimes longer and terminally funneled or knobbed. Integument with dense microtrichia, resulting in a dense stippling effect over the abdomen and pteronotum and forming transverse rows on abdominal segments IX and X. Abdominal segment IX lacking a posterior comb.

Larva I.—Cuticular color light yellow to orange. Antennal segments, tibiae, and bases of femora light brown to brown. Apices of antennal segments I and II and base and apex of III pale gray. Terminal antennal segments darker brown.

Antennae each seven segmented (Fig. 15), the suture between IV and V sometimes indistinct. Sense cones as in larva II; segment II with pair

of terminally funneled setae; segment III with six annulations with fine microtrichia present on the distal four and

some microtrichia scattered between the annulations; segment IV with five annulations, with longer microtrichia

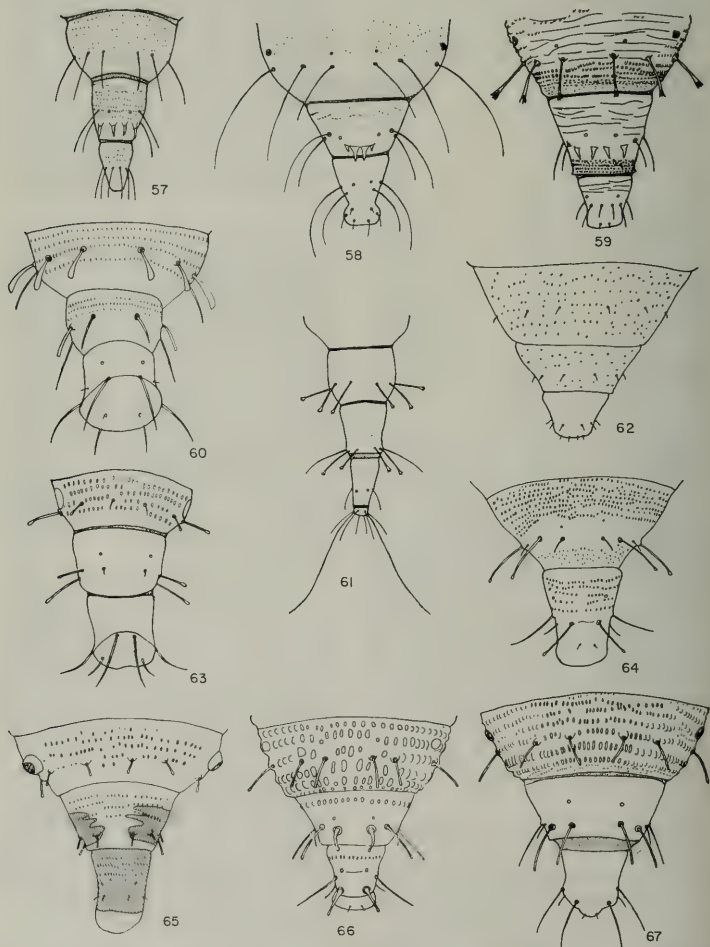


Fig. 57-67.—Abdominal segments VIII-X of the second-instar larva. 57.—*Aeolothrips vittipennis*. 58.—*Merothrips morgani*. 59.—*Heterothrips arisaemae*. 60.—*Caliothrips indicus*. 61.—Phlaeothripid (Tubulifera). 62.—*Chirothrips simplex*. 63.—*Heliethrips haemorrhoidalis*. 64.—*Limothrips cerealium*. 65.—*Hercinothrips femoralis*. 66.—*Oxythrips cannabensis*. 67.—*Anaphothrips secticornis*.

present on and randomly between the annulations; segment VII tapering apically.

Chaetotaxy similar to that of larva II, except the posteroangular setae lacking, mesonotum with four pairs and metanotum with three pairs of setae, and abdominal segment IX with two dorsal pairs and one lateral pair of setae. Integument with microtrichia, and resultant stippled pattern fainter than in larva II.

Diagnosis.—*Scirtothrips* larvae can be distinguished from the larvae of other sericothripines by their long dense cuticular microtrichia and by their simple reduced dorsal body setae, only a few of which are long and terminally funneled. *Drepanothrips* and *Sericothrips* have less dense and shorter cuticular microtrichia and all setae either terminally funneled or fanned. *Scirtothrips* resembles *Dendrothrips* in having small simple setae with only certain ones longer and terminally funneled, but larvae of the latter genus lack the dense cuticular microtrichia of *Scirtothrips*.

Morphological characters used to separate the larvae of *Scirtothrips* are uncertain. The extent of intraspecific variation in the species is not known due to a lack of specimens. Host-plant data and associated adults should be used where possible to supplement larval identifications.

KEY TO THE MATURE LARVAE II
OF SCIRTOTHRIPS

1. Dorsal setae H1, H4, P7, A(IX)2, and A(X)1 all terminally funneled; H1 and H4 both longer, about 23 μ m (Fig. 49); body color yellow; found on dogwood**niveus**
- At most, only dorsal setae H1 and P7 funneled; H1 and H4 shorter, about 15 μ m (Fig. 50); body color yellow or orange; found on red cedar or on cypress 2
2. Body color usually orange; setae A(IX)1 and 3 significantly shorter than A(IX)2; found on red cedar **brevipennis**

Body color yellow, sometimes with orange subintegral pigment; setae A(IX)1 and 3 long (19 and 23–25 μ m) and subequal to A(IX)2 (Fig. 72); found on cypress...**taxodii**

Scirtothrips brevipennis
Hood (1914)

Larva II.—Body pale orange to yellow-orange, sometimes with darker orange pigmentation. Antennal segments I–IV brown; apices of segments I, II, and III pale gray; segments V–VII darker brown. Tibiae, bases of femora, and anterior median cephalic spot brown. Eyes red.

Most setae simple, pointed, and short; H1 and P7 longer and funneled; A(IX)2 pointed and decidedly longer than A(IX)1 and A(IX)3. Cuticle with fine dense microtrichia.

Measurements of the *S. brevipennis* larva II are shown in Table 10.

Table 10.—Measurements, in microns, of two *Scirtothrips brevipennis* larvae II.

Character	Length Range	Width Range
Antennal segment		
I	17*	23
II	31	23
III	46	22
IV	46	22
V	8	14
VI	8	12
VII	15	6
Antenna	170	...
Head	93–108	78
Pronotum	90–101	140–155
Body	631	...
Setae		
H1	16	
H4	16	
P7	16–17	
A(IX)1	14–16	
A(IX)2	25–26	
A(IX)3	16	

* A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—*S. brevipennis* larvae are distinguished from those of *niveus* in having shorter cephalic setae (H1 and H4) and having H4, A(IX)2, and

A(X)1 pointed instead of terminally funneled. *S. brevipennis* larvae are separated from those of *taxodii* by having orange body color (usually yellow in *taxodii*) and shorter setae (A1 and A3) on abdominal segment IX than *taxodii* larvae have. *S. brevipennis* is found on eastern red cedar (*Juniperus virginiana*).

Material Examined.—INHS: 2 larvae II; June; on red cedar; Johnson and Pope counties, Illinois.

Scirtothrips niveus

Hood (1913)

(Fig. 49)

Larva II.—Body yellow with darker yellow pigmentation. Antennae, tibiae and bases of femora light brown. Apices of antennal segments I and II and base and apex of III pale gray. Eyes red.

Most setae simple, fairly short (12 μ m), and pointed; H1, H4, P7, A(IX)2, and A(X)1 all longer and funneled. Cuticle with fine dense microtrichia.

Measurements of the *S. niveus* larva II are shown in Table 11.

Diagnosis.—*S. niveus* larvae can be distinguished from other *Scirtothrips*

Table 11.—Measurements, in microns, of one *Scirtothrips niveus* larva II.

Character	Length	Width
Antennal segment		
I	16	25
II	29	22
III	46	22
IV	43	22
V	11	16
VI	11	11
VII	16	8
Antenna	172	...
Head	93	93
Pronotum	108	163
Body	840	...
Setae		
H1	23	
H4	23	
P7	23	
A(IX)1	20	
A(IX)2	28	
A(IX)3	23	
A(X)1	14	

larvae considered here by the longer H1 and H4 setae and by knobbed rather than pointed H4, A(IX)2, and A(X)1 setae. *S. niveus* occurs on leaves of dogwood (*Cornus* sp.).

Material Examined.—INHS: 1 larva II; June; on dogwood; Cook County, Illinois.

Scirtothrips taxodii Hood (1954)

(Fig. 15, 33, 50, and 72)

Larva II.—Body color yellow, often with red-orange body pigment. Antennae, tibiae, bases of femora, and anterior median cephalic spot light brown. Antennal segments V–VII usually darker brown. Apices of antennal segments I and II and base and apex of III pale gray. Eyes red.

Most setae pointed and short (11–12 μ m); H1, H4, P7, A(IX)2, and A(X)1 longer and knobbed. A(IX)1 and A(IX)3 long and subequal to A(IX)2. Cuticle with dense microtrichia.

Measurements of the *S. taxodii* larva II are shown in Table 12.

Table 12.—Measurements, in microns, of six *Scirtothrips taxodii* larvae II.

Character	Length		Width
	Range	Mean	
Antennal segment			
I	16–17	...	22–24
II	18–30	...	20–23
III	43–46	...	20–23
IV	43–46	...	20–23
V	6–8	...	12–16
VI	9–11	...	9–11
VII	19–23	...	8 ^a
Antenna	164–185	174	...
Head	78–85	...	93–100
Pronotum	85–125	...	140–155
Body	670–780	720	...
Setae			
H1	14–16		
H4	14–17		
P7	19–23		
A(IX)1	19		
A(IX)2	25–28		
A(IX)3	23–25		
A(X)1	20–23		

^a A single measurement in a range column indicates that all such measurements were identical.

Larva I.—Body pale yellow, often with red-orange body pigment. Antennal segments I and II light brown; segments III and proximal portion of IV brownish orange; apex of IV and seg-

ments V-VII all darker brown; tibiae and bases of femora brown. Eyes red.

Most setae pointed and short ($8\text{ }\mu\text{m}$); only H1 knobbed. Posteroangular setae lacking. Anterior median cephalic spot

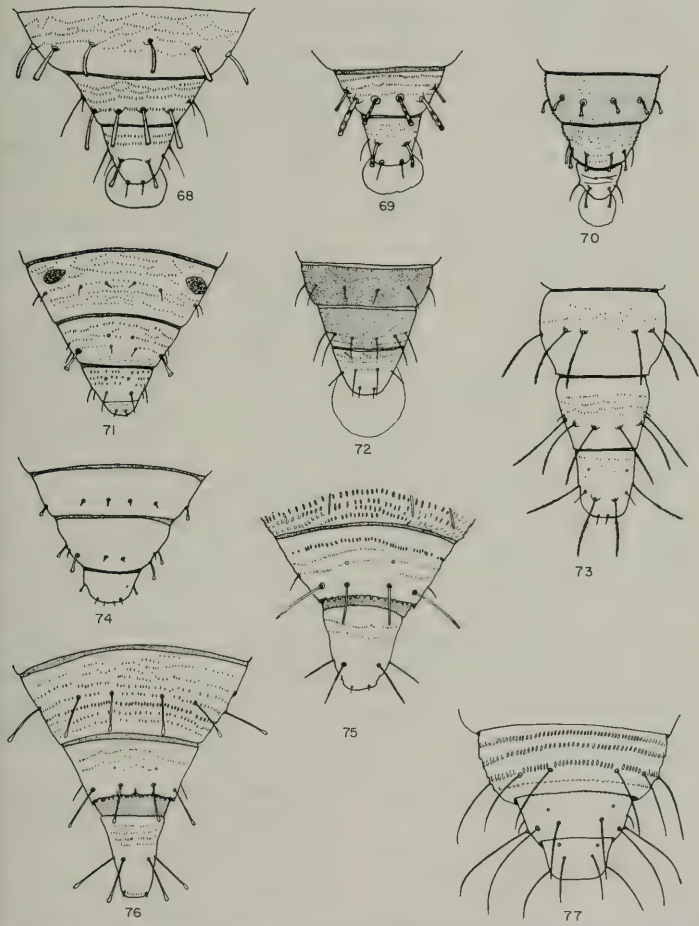


Fig. 68-77.—Abdominal segments VIII-X (except where indicated) of the second-instar larva. 68.—*Sericothrips campestris*. 69.—*Sericothrips annulipes*, abdominal segments IX and X. 70.—*Drepanothrips reuteri*. 71.—*Dendrothrips ornatus*. 72.—*Scirtothrips taxodii*. 73.—*Echinothrips americanus*. 74.—*Pseudodendrothrips mori*. 75.—*Taeniothrips simplex*. 76.—*Ctenothrips bridwelli*. 77.—*Scolothrips pallidus*.

lacking. Cuticle with very fine microtrichia.

Measurements of the *S. taxodii* larva I are shown in Table 13.

Table 13.—Measurements, in microns, of two *Scirtothrips taxodii* larvae I.

Character	Length Range	Width Range
Antennal segment		
I	12 ^a	18–20
II	18–20	19–20
III	27–30	24
IV	38–47	19–27
V	6–7	12
VI	6–7	8–9
VII	15	5–6
Antenna	120–138	...
Head	74	85
Pronotum	85	119–124
Body	527–542	...
Setae		
H1	9	
A(IX)1	13	
A(IX)2	24	
A(X)1	15	

^a A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—*S. taxodii* larvae are distinguished from *S. niveus* larvae by shorter H1 and H4 setae and by pointed instead of knobbed H4, A(IX)2, and A(X)1 setae. *S. taxodii* is differentiated from *S. brevipennis* by body color, which tends to be yellow in *taxodii* and orange in *brevipennis*, and by setae A1 and A3 on abdominal segment IX being longer and closer to the length of A2. *S. taxodii* is found on leaves of bald cypress (*Taxodium distichum*).

Material Examined.—INHS: 2 larvae I, 11 larvae II; June–August; on bald cypress; Alexander and Massac counties, Illinois.

Sericothrips Haliday (1836)

Larva II.—Body color pale yellow to yellow to yellow-orange, several species showing light to heavy orange or red hypodermal pigmentation. Antennal segments, tibiae, bases of femora,

setae, and setal basal rings (and abdominal segments IX and X in *S. annulipes*) light brown to brown. Apices of antennal segments I and II and base and apex of III pale gray. Brown sclerotized areas present on anterior median head area and, in certain species, on pteronotum. Eyes red.

Antennae each seven segmented (Fig. 31); longest sense cone on segment IV and sense cones on segments V and VI moderately long and slightly blunted, all subequal. Sense cones on segment V slightly shorter. Segments II and III each with a pair of fanned setae. Segment III with six annulations; very fine microtrichia present on the distal annulations. Segment IV with five annulations, all with longer, more prominent microtrichia.

Head (Fig. 53) wider than long. Eyes with four large facets bulging at sides of head. Mouth cone moderately blunt. Head with four pairs of dorsal setae; H1 and H4 always, and H2 and H3 sometimes, fanned; H1 directly opposite H2; H3 reduced and much smaller than H4; H4 varying from shorter than to subequal to H1.

Pronotum wider than long and with seven pairs of setae. Setae P1, 3, and 5 usually shorter, and P7 longer than P2, 4, and 6. Mesonotum with seven pairs of fanned setae, two pairs located medially and five pairs laterally. Metanotum with four pairs of fanned setae, two pairs located medially and two pairs laterally. Meso- and metanotum each with two pairs of brown sclerotized areas in *annulipes*, *pulchellus*, and *cingulatus*.

Abdominal segment I with two pairs and abdominal segments II–VIII each with three pairs of fanned setae; A1 usually shortest and A3 usually longest, their lengths varying among *Sericothrips* species. Segment IX with setae A1 and A2 long and narrowly fanned, A3 reduced and sometimes fanned. Segment X with A1 narrowly fanned.

Most dorsal body setae fanned to

varying degrees and of varying lengths. Setal bases usually with faint brown rings (much larger and more prominent in *annulipes*, *pulchellus*, and

cingulatus and to a lesser degree in *variabilis*). Integument with dense stippling resulting from very fine microtrichia; stippling forming transverse

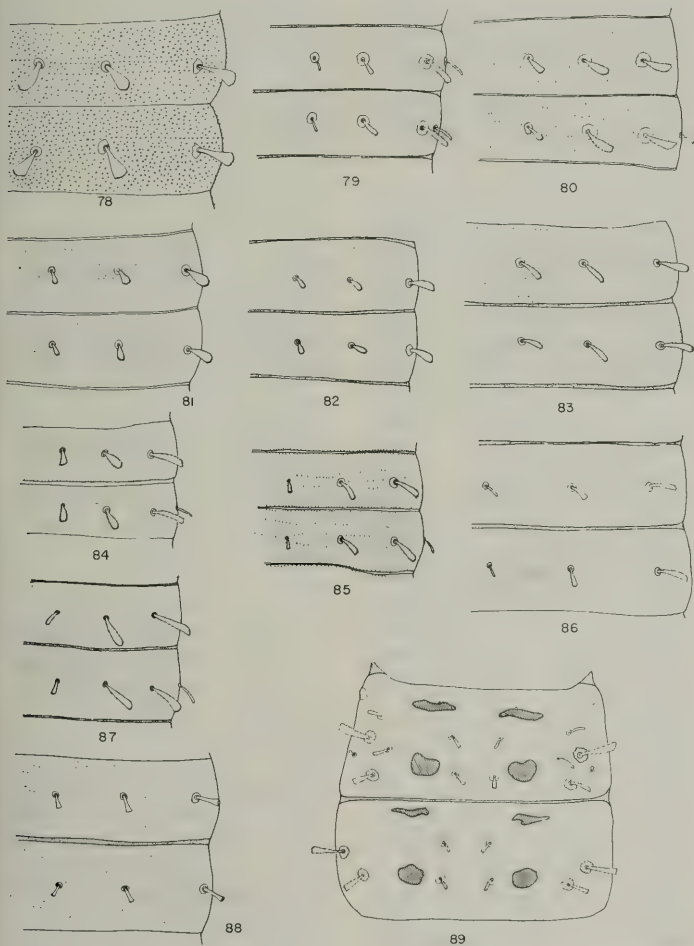


Fig. 78-89.—Abdominal segments III and IV (except where indicated) of *Sericothrips* species. 78.—*S. cingulatus*. 79.—*S. annulipes*. 80.—*S. pulchellus*. 81.—*S. variabilis*. 82.—*S. baptisiae*. 83.—*S. campestris*. 84.—*S. beachae*. 85.—*S. tiliae*. 86.—*S. nubilipennis*. 87.—*S. sambuci*. 88.—*S. langei*. 89.—*S. annulipes*, meso- and metanotum.

rows on abdominal segments, particularly on segments IX and X (minute pustules present in *cingulatus*). Abdominal segment IX lacking a posterior comb.

Larva I.—Body color pale yellow to orange-yellow, with hypodermal pigment in some species. Antennal segments, tibiae, bases of femora, and setae light brown. Apices of antennal segments I and II and base and apex of III pale gray. Terminal antennal segments darker brown.

Antennae each seven segmented, the suture between IV and V sometimes indistinct. Sense cones on segments IV and V as in larva II, but longer; sense cone on segment VI as in larva II (Fig. 14). Segments II and III each with a pair of fanned setae. Segment III with six annulations with small microtrichia present on most. Segment IV with five annulations with longer microtrichia present on and randomly between the annulations. Segment VII tapering apically.

Chaetotaxy similar to that of larva II, but setae much reduced and fanned only terminally; posteroangular setae (P7) lacking; mesonotum with four pairs and metanotum with three pairs of setae; abdominal segment IX with two dorsal pairs of fanned setae. Anterior median cephalic spot, pteronotal sclerotized areas, and raised setal basal rings all lacking. Integument with stippling as in larva II, but fainter.

Diagnosis.—*Sericothrips* larvae can be distinguished from those of all other Thripinae except *Zonothrips* by the presence of fimbriate fan-shaped setae. Larvae of *Zonothrips* were unavailable to me, but they can be separated from those of *Sericothrips* through the associated adults and host-plant data. A description and illustration of *Z. karnyi* (larva II) were given by Priesner (1926a), but this description and illustration are lacking in diagnostic characters sufficient to separate *Zonothrips* from *Sericothrips*.

Characters used to differentiate between larvae of *Sericothrips* species vary in their value. Presence or absence of large setal basal rings and brown sclerotized areas on the pteronotum are always consistent. Presence or absence of an anterior median cephalic spot and the proportions of the lengths of the abdominal dorsal setae are fairly reliable. Body color, hypodermal pigmentation, proportionate lengths of certain head and pronotal setae, and the general length and width of the setae are useful only when used in conjunction with other characters.

KEY TO THE MATURE LARVAE II OF *SERICOTHRIPS*

1. Pteronotum with brown sclerotized areas (Fig. 89); abdominal and pteronotal setae with basal rings moderately or greatly enlarged (7–15 μ m in diameter) 2
- Pteronotum lacking brown sclerotized areas; abdominal and pteronotal setae with basal rings reduced and faint (6–7 μ m in diameter) (the lateral abdominal setae with larger rings in *variabilis*) 4
2. Cuticle with microtrichia on small pustules; setal basal rings only moderately enlarged (Fig. 78) *cingulatus*
- Cuticle with microtrichia alone resulting in a stippled pattern; setal basal rings greatly enlarged 3
3. Abdominal segments IX and X usually brown; abdominal segment IV with setal pair A2 significantly shorter than A3, and A1 nearly subequal to A2 (Fig. 79); found on black locust *annulipes*
- Abdominal segments IX and X not brown; abdominal segment IV with setal pair A2 subequal to A3, and A1 significantly shorter than A2 (Fig. 80); found on wafer ash... *pulchellus*
4. Dorsal body setae generally short, the longest setae rarely exceeding 20–25 μ m and either widely or narrowly fanned; abdominal segment IV with setae A1 and A2 subequal and significantly shorter than A3... 5
- Dorsal body setae generally long, the longer setae measuring up to 30–35 μ m; proportions of abdominal setae variable 6

5. Body setae widely fanned (Fig. 82);
found on false indigo**baptisiae**
Body setae narrowly fanned (Fig.
88); found on water lily.....**langei**
6. Setal pair A2 on anterior abdominal
segments subequal to A3, the length
of A1 varying 7
Setal pair A2 on anterior abdominal
segments significantly shorter than
A3, and A1 usually significantly
shorter than A2 8
7. Setal pair A1 subequal to A2 (Fig.
83); A3 not over 25 μm long on
abdominal segment IV; found on
wild four-o'clock**campestris**
Setal pair A1 shorter than A2 (Fig.
87); A3 up to 30 μm long on abdom-
inal segment IV; found on elder-
berry**sambuci**
8. Setae generally widely fanned (Fig.
81 and 84) 9
Setae generally narrowly fanned (Fig.
85 and 86) 10
9. Lateral abdominal setae with large
basal rings (Fig. 81); body color
yellow to orange, sometimes with
red hypodermal pigmentation
.....**variabilis**
Lateral abdominal setae with reduced
basal rings (Fig. 84); body color
pale white to yellow without red
hypodermal pigmentation**beachae**
10. Body color usually white to whitish
yellow; found on various forest
trees and in forest debris..**nubilipennis**
Body color usually more yellow; found
on basswood**tiliae**

Sericothrips annulipes Hood (1927*b*)
(Fig. 31, 53, 69, and 79)

Larva II.—Body yellow with promi-
nent red-orange hypodermal pigmen-
tation dorsally in mature larvae. Anten-
nae, tibiae, bases of femora, abdominal
segments IX and X, setae, setal rings,
and cephalic spot brown. Apices of
antennal segments I and II and base
and apex of segment III pale gray.
Eyes red.

Most dorsal body setae fairly long
and fairly narrowly fanned. Longer
body setae generally twice the length
of the shorter setae; longer setae, 22–
30 μm , shorter setae, 9–16 μm . Bases
of setae with prominent raised brown

rings (7–13 μm in diameter) on ab-
domen and pteronotum. Head some-
times with a truncate apical point;
anterior median brown cephalic spot
usually present. Mesonotum and meta-
notum each with two pairs of brown
sclerotized areas (Fig. 89). Abdominal
segment IV with setal pair A1 subequal
to A2, and both significantly shorter
than A3 (Fig. 79); A1 usually shorter
than A2 on segment IX.

Measurements of the *S. annulipes*
larva II are shown in Table 14.

Table 14.—Measurements, in microns, of
10 *Sericothrips annulipes* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	48-54	...	21-22
IV	45-52	...	18-21
V	6-7	...	10-13
VI	7-9	...	7-10
VII	18-22	...	4-6
Antenna	170-189	176	...
Head	132-150	...	87-97
Pronotum	90-127	...	135-160
Body	882-1,061	995	...
Setae			
H1	25-30		
P7	25-32		
A(IV)1	9-13		
A(IV)2	13-18		
A(IV)3	24-30		
A(IX)1	22-28		
A(IX)2	28-31		
Ventral setae (IX)	9-15		

Larva I.—Body pale yellow to yel-
low. Antennal segments I–IV, legs, and
setae light brown; antennal segments
V–VII darker brown. Eyes red.

Most body setae fanned or expanded
only terminally, fimbriate for most of
their length, and shorter than in larva
II (10–20 μm in larva I). Setal basal
rings and brown sclerotized areas of
pteronotum lacking. Abdominal cuticle
with faint stippling, but more promi-
nent and forming transverse rows on
segments IX and X.

Measurements of the *S. annulipes*
larva I are shown in Table 15.

Table 15.—Measurements, in microns, of seven *Sericothrips annulipes* larvae I.

Character	Length Range	Width Range
Antennal segment		
I	14-19	19-25
II	22-28	20-25
III	28-36	22-25
IV	46-50	22-25
V	5 ^a	11-12
VI	6-8	8
VII	19-23	5
Antenna	140-169	...
Head	165-178	105-120
Pronotum	120-135	180-186
Body	571-681	...
Setae		
H1	11-12	
A(IX)1	12-19	
A(IX)2	12-20	

^a A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—*S. annulipes* larvae are similar to those of *pulchellus* and *cingulatus*. All possess brown sclerotized areas on the pteronotum and enlarged rings at the setal bases. *S. annulipes* can be distinguished from *cingulatus* by the lack of cuticular pustules and by the presence of some shorter body setae in *annulipes*. It differs from *pulchellus* by the brown color of abdominal segments IX and X and in the proportions of the anterior abdominal setae. In *annulipes* setal pair A(IV)1 is shorter than A(IV)2 and both are shorter than A(IV)3; in *pulchellus* (Fig. 80) A(IV)1 is shorter than A(IV)2, which is subequal to A(IV)3. *S. annulipes* is found on locust trees, particularly black locust, throughout the state.

Material Examined.—INHS: 14 larvae I, 10 larvae II; on black locust; Johnson, Piatt, Putnam, Stephenson, and Union counties, Illinois.

Sericothrips baptisiae Hood (1916) (Fig. 82)

Larva II.—Body yellow to yellow-orange, without hypodermal coloring. Antennae, tibiae, bases of femora,

setae, setal rings, anterior cephalic spot, and sometimes abdominal segment X light brown to brown. Apices of antennal segments I and II and base and apex of III pale gray. Eyes red.

Most setae, except H1, P7, and A(IX)1 and 2, short (22-33 μ m) and widely fanned; shorter setae, 9-13 μ m; longer setae, 15-18 μ m. Bases of setae with small unraised brown rings (6 μ m in diameter). Head with anterior median brown spot. No dorsal brown sclerotized areas on pteronotum. Abdominal segment IV with setal pair A1 subequal to A2 and both significantly shorter than A3 (Fig. 82). Stippling on abdominal segments forming irregular transverse rows.

Measurements of the *S. baptisiae* larva II are shown in Table 16.

Table 16.—Measurements, in microns, of three *Sericothrips baptisiae* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	52-55	...	22-24
IV	51-55	...	21-22
V	7 ^a	...	10-12
VI	7	...	10
VII	21-24	...	6-7
Antenna	185-202	198	...
Head	165-178	...	105-120
Pronotum	120-135	...	180-186
Body	791-889	936	...
Setae			
H1	22-25		
P7	21-24		
A(IV)1	10		
A(IV)2	10-13		
A(IV)3	18-19		
A(IX)1	21-30		
A(IX)2	29-33		
Ventral setae (IX)	15-18		

^a A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—*S. baptisiae* larvae are distinguished from other *Sericothrips* larvae by having short and widely fanned dorsal body setae and by setae A1 and A2 on abdominal segment IV being equal and significantly shorter

than A3. *S. langei* larvae are similar to *baptisiae* larvae in setal length and proportions, but have narrower setae. *S. baptisiae* is found exclusively on false indigo (*Baptisia*) throughout the state.

Material Examined.—INHS: 3 larvae II; September; on *Baptisia*; Adams and Vermilion counties, Illinois.

***Sericothrips beachae* Hood (1927a)**
(Fig. 84)

Larva II.—Body very pale yellow or white without hypodermal pigmentation. Antennae, tibiae, bases of femora, setae, and anterior cephalic spot light brown. Apices of antennal segments I and II and base and apex of III pale gray. Eyes red.

Most body setae fairly long and moderately fanned. Longer body setae (24–36 μm) about twice the length of shorter body setae (10–16 μm). Bases of setae with very faint small rings. Apex of head sometimes pointed and with an anterior median brown spot.

Table 17.—Measurements, in microns, of four *Sericothrips beachae* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	45–60	...	22*
IV	45–52	...	17–19
V	6–7	...	12
VI	7–9	...	7–9
VII	24	...	6
Antenna	157–202	189	...
Head	150–180	...	82–97
Pronotum	115–135	...	150–180
Body	725–995	890	...
Setae			
H1	30–36		
P7	29–31		
A(IV)1	9–13		
A(IV)2	12–18		
A(IV)3	18–27		
A(IX)1	31–33		
A(IX)2	31–34		
Ventral setae (IX)	18–23		

* A single measurement in a range column indicates that all such measurements were identical.

No brown sclerotized areas on pteronotum. On abdominal segment IV setal pair A1 subequal to A2 (occasionally decidedly shorter) and both significantly longer than A3 (Fig. 84). Stippling on abdominal segments faint and forming irregular transverse rows.

Measurements of the *S. beachae* larva II are shown in Table 17.

Diagnosis.—*S. beachae* larvae can be distinguished from other light-colored *Sericothrips* larvae with longer body setae by their wide body setae and by setal pair A(IV)2 being significantly shorter than A(IV)3. *S. beachae* can be distinguished from *variabilis*, a closely related species, by the total lack of any hypodermal and cuticular pigmentation and by the absence of small basal rings on lateral abdominal setae. *S. beachae* is found on hops in many areas of the state.

Material Examined.—INHS: 4 larvae II; 2 June 1970; on hops; Iroquois County, Illinois.

***Sericothrips campestris* Hood (1939)**
(Fig. 68 and 83)

Larva II.—Body usually yellowish orange without hypodermal pigmentation. Antennae, tibiae, bases of femora, setae, and setal rings brown. Antennal segment I, apex of II, and base and apex of III pale gray. Eyes red.

Setae fairly long and moderately fanned. Shorter body setae (12–22 μm) usually about two-thirds the length of longer setae (22–31 μm). Setae with faint, unraised, brown basal rings (8 μm in diameter). Apex of head obtusely pointed; anterior median cephalic spot lacking. Dorsal sclerotized areas lacking. Lengths of setae on abdominal segment IV unequal to subequal (Fig. 83). Setal pair A1 usually subequal to A2 on segment IX (Fig. 68). Stippling on abdominal segments forming definite transverse rows on terminal segments and to a lesser extent on others.

Measurements of the *S. campestris* larva II are shown in Table 18.

Table 18.—Measurements, in microns, of 10 *Sericothrips campestris* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	52-55	...	22-27
IV	48-60	...	19-23
V	6-9	...	12-14
VI	9-12	...	9-10
VII	21-24	...	6-8
Antenna	195-220	202	...
Head	112-150	...	175-210
Pronotum	147-180	...	97-120
Body	990-1,179	1,001	...
Setae			
H1	25-31		
P7	28-34		
A(IV)1	15-22		
A(IV)2	16-30		
A(IV)3	22-30		
A(IX)1	24-34		
A(IX)2	29-35		
Ventral setae (IX)	22-30		

Larva I.—Body yellow to yellow-orange. Antennae, tibiae, and setae very light brown. Antennal segment I, apex of II, and base and apex of III pale gray. Eyes red.

Most dorsal body setae fanned or expanded only terminally, fimbriate for most of their length, and shorter than

Table 19.—Measurements, in microns, of three *Sericothrips campestris* larvae I.

Character	Length		Width Range
	Range		
Antennal segment			
I	16-19		23-26
II	25-28		23-25
III	23-39		25-28
IV	46-54		23-25
V	5-8		11-12
VI	8-11		8 ^a
VII	20-22		5-6
Antenna	150-170		...
Head	62-85		78-85
Pronotum	85-93		116-140
Body	573-636		...
Setae			
H1	12-14		
A(IX)1	14		
A(IX)2	19-22		

^a A single measurement in a range column indicates that all such measurements were identical.

in larva II (10-22 μ m in larva I). Setal rings lacking. Abdominal cuticle with faint stippling, becoming more prominent on terminal segments.

Measurements of the *S. campestris* larva I are shown in Table 19.

Diagnosis.—Larvae of *S. campestris* resemble those of *sambuci* in having long setae and having setal pair A2 subequal to A3 on segment IV; A1 is subequal to A2 on segment IV in *campestris*, but is shorter in *sambuci*, and *sambuci* has slightly longer setae.

S. campestris occurs on wild four-o'clock (*Mirabilis nyctaginea*) along gravelly railroad embankments in Illinois.

Material Examined.—INHS: 3 larvae I, 12 larvae II; June-August; on wild four-o'clock; Champaign and Vermilion counties, Illinois; Lathrop, Missouri; and Ogallala, Nebraska.

Sericothrips cingulatus

Hinds (1902)

(Fig. 78)

Larva II.—Cuticle yellow to orange without hypodermal pigmentation. Antennal segments, tibiae, bases of femora, setae, setal basal rings, sclerotized areas on pteronotum, and abdominal segment X brown to dark brown. Apices of antennal segments I and II and base and apex of III pale gray.

Most dorsal body setae long and widely fanned. Bases of setae on abdomen and pterothorax with prominent brown rings (8-12 μ m in diameter). Mesonotum and metanotum each with a pair of brown sclerotized areas as in *S. annulipes* (Fig. 89). Anterior abdominal segments with dorsal setae equal or subequal (Fig. 78); A1 on segment IX subequal to A2. Abdominal stippling large, almost forming small pustules (Fig. 78).

Measurements of the *S. cingulatus* larva II are shown in Table 20.

Diagnosis.—*S. cingulatus* larvae resemble the larvae of the *annulipes*

Table 20.—Measurements, in microns, of one *Sericothrips cingulatus* larva II.

Character	Length	Width
Antennal segment		
I	23	39
II	39	29
III	59	28
IV	37	23
V	6	17
VI	12	12
VII	28	6
Antenna	204	...
Head	101	116
Pronotum	140	202
Body	1,050	...
Setae		
H1	31	
P7	28	
A(IV)1	26	
A(IV)2	29	
A(IV)3	29	
A(IX)1	31	
A(IX)2	39	
Ventral setae (IX)	12	

group of *Sericothrips* in possessing pteronotal sclerotized areas and prominent (although smaller) rings at the bases of the setae, and in having abdominal segment IX brown. *S. cingulatus* can be recognized by its dark brown body color, its having almost all dorsal body setae long and equal or subequal, and the presence of small pustules.

Larval and adult morphology of *cingulatus* indicate that this species is atypical of most *Sericothrips*. Adults of *cingulatus* possess dense abdominal microtrichia completely covering the tergites, whereas the tergites of most species in this genus possess microtrichia only laterally. In the larvae the cuticular stippling is modified into small pustules, and the brown sclerotized areas are similar to those found in the more primitive Chirothripini.

S. cingulatus is found scattered statewide in grassland areas and particularly in grass-sedge marshes.

Material Examined.—INHS: 1 larva II; 18 March 1971; on clover and vetch; Amite, Louisiana.

Sericothrips langei Moulton (1929) (Fig. 88)

Larva II.—Body white to light yellow, sometimes light orange, without subintegumental pigmentation. Antennae, tibiae, bases of femora, setae, and setal rings light brown. Most of antennal segment I, the apex of II, and the base and apex of III pale gray. Eyes red.

Most body setae short and all narrowly expanded. Shorter body setae (7–13 μm) usually about one-half the length of longer setae (13–24 μm). Setae with small faintly brown unraised rings (6 μm in diameter). Head often with an apical point. Anterior cephalic spot lacking. Abdominal segment IV with setal pair A1 subequal to A2 and both significantly shorter than A3 (Fig. 88). Setal pair A1 on segment IX significantly shorter than A2. Stippling on abdomen forming prominent transverse rows on the terminal segments, becoming less prominent on the others.

Measurements of the *S. langei* larva II are shown in Table 21.

Table 21.—Measurements, in microns, of nine *Sericothrips langei* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	48–55	...	22–27
IV	21–23	...	21–23
V	7–12	...	13–15
VI	10 ^a	...	10–12
VII	22–30	...	6–7
Antenna	202–227	214	...
Head	180–190	...	123–130
Pronotum	123–140	...	180–202
Body	901–1,159	1,040	...
Setae			
H1	18–22		
P7	25–31		
A(IV)1	7–11		
A(IV)2	8–15		
A(IV)3	15–24		
A(IX)1	13–17		
A(IX)2	18–25		
Ventral setae (IX)	12–15		

^a A single measurement in a range column indicates that all such measurements were identical.

Larva I.—Body light yellow to yellow-orange. Antennal segments I–IV, tibiae, and setae very light brown; antennal segments V–VII darker brown. Eyes red.

Most body setae expanded only terminally and shorter than those of larva II (6–15 μ m in larva I). Setal rings lacking. Cuticle with faint stippling becoming more prominent on the terminal segments.

Measurements of the *S. langei* larva I are shown in Table 22.

Diagnosis.—*S. langei* larvae can be distinguished from all other *Sericothrips* larvae considered here by the very short and very narrowly fanned setae. The species is found on water lilies of the genus *Nymphaea* throughout the state.

Material Examined.—INHS: 5 larvae I, 20 larvae II; June–August; on water lily; Lake and Monroe counties, Illinois, and Au Train, Michigan.

Table 22.—Measurements, in microns, of four *Sericothrips langei* larvae I.

Character	Length Range	Width Range
Antennal segment		
I	16–19	26–28
II	28–31	23–26
III	31–37	25–28
V	5–6	11–12
VI	9–12	8 ^a
VII	20–25	5
Antenna	162–174	...
Head	85–100	93–100
Pronotum	85–124	140
Body	642–734	...
Setae		
H1	9–12	
A(IX)1	8–9	
A(IX)2	14–16	

^a A single measurement in a range column indicates that all such measurements were identical.

Sericothrips nubilipennis

Hood (1924)

(Fig. 86)

Larva II.—Body whitish yellow without hypodermal pigmentation. Anten-

nae, tibiae, and setae light brown. Antennal segment I, base of II, and base and apex of III pale gray. Eyes red.

Setae fairly long and moderately fanned. Shorter body setae (12–18 μ m) generally two-thirds the length of the longer setae (19–31 μ m). Setae with very faint basal rings (6 μ m in diameter). Apex of head usually rounded; median anterior spot lacking. Dorsal sclerotized areas lacking. Abdominal segment IV with all setae varying from decidedly unequal to subequal in certain cases (Fig. 86). Setal pair A1 of segment IX usually shorter than A2. Abdominal stippling generally faint, transverse rows being prominent mainly on the terminal segments.

Measurements of the *S. nubilipennis* larva II are shown in Table 23.

Table 23.—Measurements, in microns, of five *Sericothrips nubilipennis* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	45–55	...	20–22
IV	48–60	...	18–21
V	7–13	...	12–15
VI	10–12	...	9–10
VII	26–30	...	5–7
Antenna	189–214	202	...
Head	135–165	...	90–112
Pronotum	112–135	...	157–202
Body	850–1,033	932	...
Setae			
H1	30–31		
P7	23–36		
A(IV)1	10–18		
A(IV)2	12–22		
A(IV)3	18–25		
A(IX)1	22–30		
A(IX)2	22–31		
Ventral setae (IX)	15–22		

Diagnosis.—Larvae of *S. nubilipennis* are distinguished by their narrowly fanned setae and by A(IV)2 being significantly shorter than A3. This species is similar to and often indistinguishable from *S. tiliae*. The body color of *nubilipennis* tends to be white, whereas that of *tiliae* tends to be yellow.

low. Host-plant data are unreliable criteria, too, since both species can occur on adjacent forest plants with accidental transfers being made from one host to the other.

S. nubilipennis generally occurs on various forest trees, such as hackberry (*Celtis*) or dogwood (*Cornus*) throughout the state.

Material Examined.—INHS: 5 larvae II; June–October; on hackberry leaves and forest leaf litter; Champaign, Henderson, Macon, and Piatt counties, Illinois.

***Sericothrips pulchellus* Hood (1908)**
(Fig. 80)

Larva II.—Cuticle orange with prominent red-orange hypodermal pigmentation, often faint. Antennae, tibiae, bases of femora, setae, setal rings, anterior cephalic spot, and dorsal sclerotized pteronotal areas light brown to brown. Apices of antennal segments I and II and base and apex of III gray.

Table 24.—Measurements, in microns, of 10 *Sericothrips pulchellus* larvae II.

Character	Length		Width
	Range	Mean	Range
Antennal segment			
III	44–52	...	22 ^a
IV	44–52	...	20–22
V	7	...	12–15
VI	10	...	10–13
VII	24–30	...	7
Antenna	160–189	176	...
Head	150–165	...	97–112
Pronotum	97–142	...	150–210
Body	867–1,128	945	...
Setae			
H1	27–32		
P7	30–32		
A(IV)1	12–18		
A(IV)2	19–27		
A(IV)3	22–30		
A(IX)1	21–30		
A(IX)2	27–33		
Ventral setae (IX)	15–18		

^a A single measurement in a range column indicates that all such measurements were identical.

Most dorsal body setae fairly long and moderately fanned. Shorter body setae (12–20 μm) usually two-thirds the length of the longer setae (22–31 μm). Bases of setae with prominent, raised brown rings (7–15 μm in diameter) on abdomen and pterothorax. Head usually without an apical point; anterior median cephalic spot present. Mesonotum and metanotum each with a pair of brown sclerotized areas. Abdominal segment IV with setal pair A2 subequal to A3 and both significantly longer than A1 (Fig. 80). Setal pair A1 on segment IX usually shorter than A2. Abdominal stippling forming prominent transverse rows on most abdominal segments (Fig. 80).

Measurements of the *S. pulchellus* larva II are shown in Table 24.

Larva I.—Body orange. Antennae and setae generally light brown. Apex of antennal segment IV and all of segments V–VIII brown. Eyes red.

Body setae expanded terminally and shorter than in larva II (9–25 μm in larva I). Setal basal rings, cephalic spot, and sclerotized pteronotal areas lacking. Abdominal stippling faint.

Table 25.—Measurements, in microns, of five *Sericothrips pulchellus* larvae I.

Character	Length Range	Width Range
Antennal segment		
I	11–16	23–25
II	23–25	22–23
III	26–31	23–26
IV	42–48	23–26
V	5–6	9–12
VI	8–9	8 ^a
VII	22–25	5
Antenna	150–158	...
Head	70–78	78–85
Pronotum	70–85	101–132
Body	496–611	...
Setae		
H1	11–19	
A(IX)1	19–25	
A(IX)2	12–16	

^a A single measurement in a range column indicates that all such measurements were identical.

Measurements of the *S. pulchellus* larva I are shown in Table 25.

Diagnosis.—*S. pulchellus* larvae can be distinguished from all other *Sericothrips* larvae considered here except *annulipes* and *cingulatus* by the large raised rings at the bases of the setae and by the brown sclerotized areas on the pteronotum. Red hypodermal pigmentation is also characteristic of this species although it is sometimes faint or absent.

S. pulchellus can be distinguished from *cingulatus* by the absence of cuticular pustules and by some body setae being shorter than others. *S. pulchellus* differs from *annulipes* in the absence of brown coloration on abdominal segments IX and X and in the length proportions of setae on abdominal segment V; in *annulipes* setal pair A1 is subequal to A2 and both are shorter than A3; in *pulchellus* A2 is subequal to A3 and both are longer than A1.

S. pulchellus is found on wafer ash (*Ptelea*), sometimes in great numbers. Adults and larvae feed together, often causing the foliage to turn white because of the feeding scars. At times of great abundance, adults may be scattered and found resting on a variety of trees and shrubs (Stannard 1968).

Material Examined.—INHS: 6 larvae I, 23 larvae II; June–August; on wafer ash; Carroll, Kankakee, Mason, and Winnebago counties, Illinois.

Sericothrips sambuci Hood (1924)

(Fig. 87)

Larva II.—Body yellow. Antennal segments I and II yellow; segments III–VII and setae light brown. Base and apex of antennal segment III pale gray. Eyes red.

Most body setae long and moderately fanned. Shorter body setae (10–16 μ m) usually less than half the length of longer setae (24–29 μ m). Bases of setae without rings. Apical cephalic point, median cephalic spot, and dorsal

sclerotized areas lacking. Abdominal segment IV with setal pair A2 subequal to A3 and much longer than A1 (Fig. 87); A1 on segment IX subequal to A2. Abdominal stippling forming fine transverse rows.

Measurements of the *S. sambuci* larva II are shown in Table 26.

Table 26.—Measurements, in microns, of 10 *Sericothrips sambuci* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	48–60	...	22–26
IV	51–60	...	21–33
V	7–10	...	13–15
VI	10–13	...	10–13
VII	27–32	...	6–7
Antenna	202–233	220	...
Head	150–180	...	98–120
Pronotum	120–142	...	165–202
Body	900–1,216	1,046	...
Setae			
H1	30–39		
P7	30–42		
A(IV)1	10–15		
A(IV)2	24–31		
A(IV)3	25–33		
A(IX)1	27–36		
A(IX)2	30–42		
Ventral setae (IX)	22–30		

Larva I.—Body yellow. Antennal segments I–IV pale brown; apex of IV, all of V–VII, and setae light brown. Eyes pale red.

Body setae fairly long and expanded terminally; setae generally shorter than in larva II (10–25 μ m in larva I). Stippling on abdominal cuticle faint.

Measurements of the *S. sambuci* larva I are shown in Table 27.

Diagnosis.—Larvae of *S. sambuci* resemble those of *campestris* in having long setae and A(IV)2 subequal to A(IV)3. However, A(IV)1 is subequal to A(IV)2 in *campestris* and shorter than A2 in *sambuci*.

S. sambuci is found statewide on elderberry (*Sambucus*).

Material Examined.—INHS: 1 larva I, 17 larvae II; August–October; on

Table 27.—Measurements, in microns, of one *Sericothrips sambuci* larva I.

Character	Length	Width
Antennal segment		
I	16	26
II	28	26
III	34	26
IV	50	26
V	5	12
VI	8	9
VII	23	4
Antenna	160	...
Head	78	78
Pronotum	93	124
Body	621	...
Setae		
H1	21	
A(IX)1	16	
A(IX)2	19	

Sambucus; Calhoun, Iroquois, Marion, and Union counties, Illinois.

Sericothrips tiliae Hood (1931)
(Fig. 85)

Larva II.—Body yellow (dark orange in one specimen). Antennae, legs, and setae uniformly light brown. Eyes red.

Table 28.—Measurements, in microns, of seven *Sericothrips tiliae* larvae II.

Character	Length		Width
	Range	Mean	
Antennal segment			
III	52-56	...	22-24
IV	49-57	...	16-22
V	7-9	...	13-15
VI	9-12	...	9-12
VII	23-30	...	7 ^a
Antenna	189-214	202	...
Head	135-180	...	90-107
Pronotum	105-135	...	157-172
Body	838-1,014	882	...
Setae			
H1	30-36		
P7	27-34		
A(IV)1	9-13		
A(IV)2	15-18		
A(IV)3	24-29		
A(IX)1	24-30		
A(IX)2	27-35		
Ventral setae (IX)	9-12		

^a A single measurement in a range column indicates that all such measurements were identical.

Most dorsal body setae fairly long and moderately fanned; longer setae (22-33 μ m) usually twice the length of shorter setae (9-18 μ m). Anterior median cephalic spot, brown pteronotal areas, and setal basal rings all lacking. Abdominal segment IV with setal pair A(IV)1 shorter than A(IV)2, and A(IV)2 shorter than A(IV)3 (Fig. 85); A1 on segment IX subequal to A2.

Measurements of the *S. tiliae* larva II are shown in Table 28.

Larva I.—Body yellow. Antennal segments I-IV and setae light brown; segments V-VII darker brown. Eyes red. Setae only slightly expanded and 5-17 μ m long.

Measurements of the *S. tiliae* larva I are shown in Table 29.

Table 29.—Measurements, in microns, of one *Sericothrips tiliae* larva I.

Character	Length	Width
Antennal segment		
III	36	20
IV	50	20
V	6	11
VI	8	8
VII	14	5
Antenna	165	...
Head	78	70
Pronotum	85	110
Body	622	...
Setae		
H1	9	
A(IX)1	9	
A(IX)2	17	

Diagnosis.—Larvae of *S. tiliae* are distinguished by their narrowly fanned setae and by A(IV)2 being significantly shorter than A(IV)3. This species is similar to and often indistinguishable from *S. nubilipennis*. The body color of *tiliae* is usually yellow, whereas that of *nubilipennis* is usually white.

S. tiliae is found statewide on linden (*Tilia*), being most common in the northern part of the state.

Material Examined.—INHS: 1 larva I, 8 larvae II; July-September; on linden; Effingham and Kankakee counties, Illinois.

Sericothrips variabilis (Beach 1896)
(Fig. 14, 32, and 81)

Larva II.—Body color white, changing to yellow and orange with increasing maturity of larva; red hypodermal pigment occasionally present in mature larva. Antennae, tibiae, setae, setal rings, and anterior median cephalic spot brown. Antennal segment I, apex of II, and base and apex of III pale gray. Eyes red.

Most dorsal body setae moderate in length and moderately fanned. Shorter body setae (13–19 μ m) between one-half and two-thirds the length of the longer setae (25–33 μ m). Bases of pteronotal and abdominal setae with small, faint brown rings (6 μ m in diameter); the lateral abdominal setae with larger (8 μ m in diameter) and more prominent rings. Anterior median cephalic spot present but often not visible in balsam mounts. Brown pteronotal areas lacking. Abdominal segment IV with setae A1, A2, and A3 progressively longer (Fig. 81); segment IX with A1 usually subequal to A2.

Table 30.—Measurements, in microns, of 10 *Sericothrips variabilis* larvae II.

Character	Length		Width Range
	Range	Mean	
Antennal segment			
III	53–55	...	22–24
IV	48–55	...	18–21
V	7–9	...	10–13
VI	10–12	...	9–10
VII	25–27	...	6–7
Antenna	189–202	195	...
Head	142–165	...	105–112
Pronotum	120–150	...	165–195
Body	882–1,089	1,021	...
Setae			
H1	30–31		
P7	29–39		
A(IV)1	12–19		
A(IV)2	15–24		
A(IV)3	22–31		
A(IX)1	25–31		
A(IX)2	30–34		
Ventral setae (IX)	8–11		

Measurements of the *S. variabilis* larva II are shown in Table 30.

Larva I.—Body color white to yellow. Antennal segments I–IV light brown; apex of IV and all of V–VII darker brown; apices of segments I and II and base and apex of III pale gray. Setae expanded terminally and measuring 6–16 μ m. Anterior median cephalic spot and setal rings lacking.

Measurements of the *S. variabilis* larva I are shown in Table 31.

Table 31.—Measurements, in microns, of five *Sericothrips variabilis* larvae I.

Character	Length Range	Width Range
Antennal segment		
III	30–34	25–26
IV	46–50	22–26
V	5–6	11–12
VI	8 ^a	6–9
VII	20–22	5
Antenna	158–171	...
Head	54–85	78–85
Pronotum	78–101	115–132
Body	490–621	...
Setae		
H1	9–12	
A(IX)1	11–12	
A(IX)2	16–20	

^a A single measurement in a range column indicates that all such measurements were identical.

Diagnosis.—Larvae of *S. variabilis* resemble those of *beachae* in having wider setae and A(IV)2 shorter than A(IV)3. From *beachae*, *variabilis* can be distinguished by the larger lateral setal basal rings and by often having cuticular and hypodermal coloration.

S. variabilis occurs statewide on many legumes, particularly soybeans. Its life history is discussed earlier in this report.

Material Examined.—INHS: 24 larvae I, 74 larvae II; August; on and reared from soybeans; Champaign County, Illinois.

Zonothrips Priesner (1926a)

Larva II.—Cuticle yellow, generally with red hypodermal pigment. Eyes

red. Antennae, setae, and probably tibiae and bases of femora light brown.

Antennae six (possibly seven) segmented; segments II and III each with a pair of fanned setae; segment III with six annulations, all with microtrichia.

Head constricted below eyes and longer than wide. Eyes with four large round facets bulging at sides of head. Head with four pairs of dorsal setae, H2 fanned. Pronotum with seven pairs of expanded setae. Mesonotum with seven pairs and metanotum with four pairs of fanned setae. Abdomen with two pairs of expanded setae on tergite I and three pairs on tergites II–VIII; segment IX with three pairs of dorsal setae, A1 and A2 both being fanned and A3 pointed and reduced. Segment X with three pairs of dorsal setae, A1 fanned.

Major dorsal body setae all moderately to widely fanned and moderately long. Cuticle with fine stippling probably resulting from fine microtrichia. Abdominal segment IX lacking a posterior comb.

Larva I.—Cuticle yellow without hypodermal pigmentation. Eyes red. Antennae six segmented; segments II and III with weakly expanded setae.

Chaetotaxy similar to that of larva

II, but posteroangular setae lacking, and setae shorter and less expanded. Cuticular sculpture similar to that of larva II, but fainter. Abdominal segment IX lacking a posterior comb.

Diagnosis.—This description of the genus *Zonothrips* is based on a description and illustration by Priesner (1926a) of *Z. karnyi*. *Zonothrips* can be distinguished easily from all other thripine genera except *Sericothrips* by the widely fanned, dorsal body setae. Differentiation of *Zonothrips* and *Sericothrips* is more difficult. Stannard (1968) reported the adults of these two genera as being similar, only separated by the number of antennal segments and the placement of abdominal sternal setae. The only way of separating the two genera at the present time is by considering host-plant data and associated adults.

Zonothrips osmundae

Crawford, J.C. (1941)

No larvae of this genus and species were available for study. Adults were collected in Illinois at Volo Bog, Lake County, from September to October on and around cinnamon fern (*Osmunda cinnamomea*) by L. J. Stannard, Jr., and are deposited at the Illinois Natural History Survey.

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ILLINOIS
Natural History Survey
BULLETIN

Root Infection
of Woody Hosts with
Verticillium albo-atrum

Gold L. Born

NATURAL HISTORY SURVEY

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STATE OF ILLINOIS
DEPARTMENT OF REGISTRATION AND EDUCATION

NATURAL HISTORY SURVEY DIVISION
URBANA, ILLINOIS

VOLUME 31, ARTICLE 6

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**OF ILLINOIS
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**URAL HISTORY SURVEY DIVISION
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**VOLUME 31, ARTICLE 6
AUGUST, 1974**

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Root Infection of Woody Hosts with Verticillium albo-atrum

Gerald L. Born

VERTICILLIUM WILT is a plant disease caused by the fungus *Verticillium albo-atrum* Reinke and Berthold. This pathogen is peculiar in that it does not confine its attacks to one host, or a few closely related hosts, as is so frequently the case with most other pathogenic fungi; it attacks a large number of widely unrelated plants, many of which are of economic importance. The disease does not often occur in forest stands, but it is becoming increasingly prevalent in plantings of ornamental trees and shrubs, particularly in temperate regions of the world.

Symptoms of *Verticillium* wilt on woody hosts are variable and often difficult to recognize. Usually the first visual symptom is sudden wilting of foliage on one or several twigs on a branch. A yellowing of foliage sometimes precedes wilting. Most plants exhibit leaf symptoms in early July, but some trees may first show symptoms in early spring or late fall. Leaves on affected ash species may drop while still green and before noticeable yellowing or wilting has occurred.

Other symptoms suggesting *Verticillium* wilt are decline in current twig growth, stunting, and dieback of individual twigs and branches. Occasionally trees such as maple and tulip tree develop elongated dead areas of bark on the diseased branches or trunk. Water-soaked areas sometimes develop under the killed bark.

Trees that develop a limited amount of branch wilt during the summer may show additional wilt and dieback the following year, and others may recover and not wilt in succeeding years. Trees that have extensive wilt throughout the crown usually die before the end of the summer.

The present study initiated in 1970 and completed in 1972 deals with (1) the influence of root wounds and age of wounds on infection, (2) penetration and development of the fungus in susceptible and resistant woody hosts, (3) analysis of the growth response of young tree seedlings after root infection, (4) the influence of temperature and heat treating of soil on development of *V. albo-atrum* in excised roots, and (5) laboratory and greenhouse evaluation of fungicides against *V. albo-atrum*.

This report is adapted from a thesis submitted to the University of Illinois in partial fulfillment of requirements for the degree of Doctor of Philosophy in Plant Pathology.

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LITERATURE REVIEW

The first reference to a wilt disease was made by Reinke & Berthold (1879). They isolated a fungus from potato plants with the Krauselkrankheit disease which they named *Verticillium albo-atrum*. Their investigations were not appreciated until 30 years later when *Blattrollkrankheit* and *Krauselkrankheit* were causing severe losses in the potato fields of Europe.

Van Hook (1904) described a typical case of wilt in ginseng (*Panax quinquefolium* L.) which he attributed to *Acrostalagmus albus* Preuss. However, this name is synonymous with the earlier name *Verticillium* which was established by Nees von Esenbeck (1816). Corda (1838) did not describe the genus *Acrostalagmus* until 1838.

Klebahn (1913) isolated a *Verticillium* from dahlia plants which he considered distinct from *V. albo-atrum*, and he named this fungus *V. dahliae* Kleb. Since 1913 the relationship between *V. albo-atrum* and *V. dahliae* has been the subject of much controversy. Many investigators have disagreed in their interpretations of the drawings and descriptions found in previous reports. Wollenweber (1929), Rudolph (1931), Presley (1941), Wilhelm & Taylor (1965), and Van den Ende (1958) maintained that the fungi that produce sclerotia and resting mycelium are members of a large variable species. Others, e.g., Klebahn (1913), Van der Meer (1925), Isaac (1949), and Smith & Walker (1930), have preferred to treat them as separate species.

In 1957 *Verticillium* wilt was reported as affecting plants in at least 18 orders, 38 families, 98 genera, and 137 species in the temperate climates of the world (Caroselli 1957).

Numerous papers in the past have

dealt with factors that influence the incidence of *Verticillium* wilt. Nutrition, soil type, soil moisture, soil and air temperature, and light have all been shown to have an effect on the incidence of this disease (Arndt 1957; Edgington & Walker 1957; Gallegly 1949; Gilman 1916; Ludbrook 1933; Wilhelm 1950).

Although many workers have mentioned wounds as a source of entry by pathogenic fungi into the root system, little work has been done on the problem. Selman & Buckley (1959) suggested that root injury facilitated fungus invasion and that deliberate injury with a scalpel was less harmful than normal transplanting. Their study made with transplanted seedlings, or with plants damaged by cutting, gave clear evidence that exposing injured roots to a conidial suspension of the fungus resulted in rapid systemic invasion of the host. Selman & Pegg (1957) failed to show any appreciable increase in infection as a result of deliberate root damage but, in these cases, the "undamaged" control plants had been transplanted. Under normal conditions of root growth in soil, where the inoculum potential of the fungus may be expected to be relatively low, it seems probable that entry into the xylem vessels occurs largely through wounds.

Armstrong & Armstrong (1958) found that a high incidence of infection occurred when roots of herbaceous hosts were cut prior to inoculation with *Fusarium* spp. Also, the average number of days for wilt to occur significantly decreased when roots were cut immediately prior to inoculation. Fulton (1952) showed that more infection occurred when the canes or roots of raspberry were injured prior to inoculation.

Little has been reported on the anatomy of woody hosts affected with *Verticillium* wilt. Extensive histological work has been done on herbaceous hosts attacked by this pathogen. Ru-

dolph (1931) reported that the fungus was found only in the xylem in the early wilt stage, and later invaded the pith, cambium, and cortex in the advanced wilt stages. McWhorter (1962), working with *Pelargonium* infected with *V. albo-atrum*, found only traces of mycelium in tissues that had considerable discoloration. He rarely found large amounts of mycelium in diseased tissue. Therefore, the amount of mycelia in the vessels is not always indicative of the severity of wilt.

Talboys (1958) observed that acute symptoms of hop wilt were associated with extensive development of mycelium in the xylem vessels but sparse production of tyloses; conversely, mild symptoms were associated with the development of limited mycelium but abundant tyloses in the vessels. Talboys (1964) suggested a simple explanation of the inverse correlation he had found between density of mycelium and frequency of tyloses in infected xylem vessels of the hop plant by postulating that a low concentration of fungal metabolites in the xylem stimulates the formation of tyloses but that a high concentration inhibits formation.

Until recently, spread of the fungus throughout the plant has received little attention. Sewell & Wilson (1964) concluded that *V. albo-atrum* conidia are transported in xylem sap of hops and occasionally they become lodged in vessels where they germinate and produce more conidia. In cotton and tomatoes, conidia may spread throughout the plant in 12 hours to 6 days following inoculation (Garber 1957; Green 1954).

Many earlier workers noted that the hyphae are very slender and reduced in diameter at the point where they pass through the cell walls, but once through they swell to a much greater size (Garber 1957; Garber & Houston 1966; Klebahn 1913; Reinke & Berthold 1879). In the vascular system, the

fungus moves from one vessel element to another through pits (Garber 1957; Garber & Houston 1966; Green 1954). There is an apparent inability of the mycelium to penetrate new cellular growth lateral to the invaded cells as rapidly as the new cells are formed (Green 1954).

Klebahn (1913) and Rankin (1914) reported microsclerotia in the vessels of infected plants. Talboys (1958) observed that penetration of vascular tissue of hop by *V. albo-atrum* depended on the amount of suberin in the endodermal cell walls. Garber & Houston (1966) observed gum-like deposits in tolerant cotton plants which impeded the fungus from penetrating the vascular element. They reported that the splitting apart of cells was a mechanical process and not enzymatic although they observed enzymatic action on the middle lamella of cell walls when the inoculum potential was high.

Symptom appearance is variable, requiring days to many weeks after infection for expression. Yellowing of foliage and sudden wilting are usually the first visual symptoms. General stunting accompanied by shortening of the internodes may accompany wilt. Young tomato plants infected with *V. albo-atrum* may show neither leaf yellowing nor wilting in the initial stages, but only a stunting of the whole plant (Selman & Pegg 1957).

Selman & Pegg (1957) found that 8 weeks after inoculation the dry weights of tomato leaves, stems, and roots were decreased by 72, 70, and 65 percent respectively. Of the growth characteristics studied, leaf area was most reduced by infection and this was due to a failure of the leaves to expand rather than to a reduction in leaf production.

After infection, symptom development, and necrosis, the fungus may overwinter within the plant as microsclerotia. Benken & Khakimov (1964) observed abundant microsclerotia of *V.*

albo-atrum in veins and petioles of overwintering cotton leaves. The fungus spread unchecked in the field within the necrotic tissues of infected cotton seedlings and sporulated freely over the surface of the stems for a short distance above ground level, eventually forming numerous microsclerotia in stems and roots. Nadakavukaren (1965) observed that *V. albo-atrum* microsclerotia survived best at low temperatures and high moisture levels. Heale & Isaac (1963) reported that resting mycelium remained viable for 9 months in pieces of necrotic lucerne buried 12 inches (30 cm) in soil. Brinkerhoff (1969) observed that microsclerotia were elongated in leaves incubated at 28 to 30 C and round in leaves incubated at 18 C. *V. albo-atrum* survived for relatively long periods in cotton tissue, and infested debris constituted a ready source of inoculum when incorporated into either sterile or nonsterile soil. Evans et al. (1966) suggested that further colonization by *V. albo-atrum* was arrested when cotton plants were plowed under prior to microsclerotial formation in the tissues.

Many recent papers have shown the value of systemic fungicides for the control of vascular wilts. Most of the work has been done with Benlate (benomyl) and thiabendazole (TBZ). Schreiber et al. (1971) found that benomyl was taken up equally well when either applied as a drench or incorporated directly into the potting media. The planting medium affected the concentration as well as the rate of accumulation of benomyl. Highest levels of accumulation of the fungitoxicant were in seedlings grown in media that had the lowest content of organic matter and the highest pH. Heat sterilization of soil prior to benomyl treatment resulted in greater accumulation of benomyl in elm seedlings than when the plants were grown in nonsterile soil.

Erwin et al. (1971) found that the

addition of thiabendazole to soil reduced the incidence and severity of cotton wilt in plants subsequently inoculated with *V. albo-atrum*. Rawlins & Booth (1968) reported that the addition of surfactant Tween 20 increased the effectiveness of benomyl and thiabendazole against *V. albo-atrum*, probably by increased absorption of the fungicide by the roots. Erwin et al. (1968) found that thiabendazole not only translocates from the roots to the stems of cotton plants but also can be detected in the bark. They concluded that thiabendazole diffused laterally from the xylem to the bark.

Soil treatment, or seedling root dips with difolatan (Bankuti 1964) gave good control of *Fusarium oxysporum* f. sp. *lycopersici* and *V. albo-atrum* on tomatoes in greenhouse and field tests. Complete protection against *V. albo-atrum* was provided for seedlings planted up to 140 days in soil treated with difolatan.

Applying systemic fungicides to the foliage and allowing the chemical to be translocated downward may be the method used in the future. However, this method presents many problems. Many fungicides, such as benomyl, are extremely insoluble in water. Hock (personal communication) has been able to solubilize benomyl using inorganic acids, heat, and constant stirring. Buchenauer & Erwin (1971) found that benomyl and thiabendazole induced curative effects when sprayed on inoculated cotton plants that showed initial symptoms of Verticillium wilt. Both fungicides were detected by bioassay and chemical analysis in xylem tissue and in nontreated stems and leaves above the place of application.

CODE OF VERTICILLIUM ALBO-ATRUM ISOLATES

MATERIALS AND METHODS

All isolates used throughout this study were obtained from actively wilt-

ing hosts in Illinois. They were maintained on freshly prepared potato dextrose agar (PDA) tube slants and transferred periodically. An isolate used to inoculate a particular species was obtained earlier from another of the same species. Resistant species were inoculated with a mixture of all isolates. Below are the code numbers used in this study to identify each isolate. Also, the host, date of isolation, and location of host plant in Illinois are given for each isolate.

Code	Host	Date	Place
1	Sugar maple	1969	Urbana
2	Russian olive	1956	Wheaton
3	Redbud	1960	Urbana
4	Green ash	1961	Decatur

RELATIONSHIP OF ROOT WOUNDS & AGE OF WOUNDS ON INFECTION

MATERIALS AND METHODS

Two hundred twenty each of 2-year-old bare-rooted sugar maples (*Acer saccharum* Marsh.) and redbud (*Cercis canadensis* L.) seedlings were selected as test plants. The plants were breaking dormancy when received from a commercial nursery. The average height was 45 to 60 cm. The roots of each plant were washed with tap water and rinsed with distilled water prior to planting. The plants were potted in a medium-grade perlite and fertilized bi-weekly with a balanced liquid fertilizer.

Isolate 1 was used to inoculate sugar maple and Isolate 2 was used to inoculate redbud.

Type of Wound

Two weeks after potting, 100 plants were removed from the perlite and treated. Treatments immediately preceding inoculation included: (1) no wound, (2) abrasion, (3) puncture, and (4) vascular incision. Wounds were made on the primary root approximately 5 cm below the ground line. With the abrasion-type wound,

the root surface was injured by rubbing moist 400 grade carborundum against the root surface. Puncture wounds were made by forcing a balsam wood block, in which five pins were embedded, against the root. This produced pin prick wounds 3 mm deep into the root. The vascular incisions were made by cutting a V-shaped wedge approximately 0.5 cm deep into the root. When no wound was made, a mycelial disc was placed against the root surface.

All treated plants were inoculated with a mycelial disc and the wound area covered with vinyl grafting tape to prevent moisture loss. The control plants were treated identically except that a sterile agar disc was placed on the wounded area and covered with grafting tape. Twenty plants of each species were used for each treatment.

After 30 days, all plants were removed from the pots and isolations were attempted from the plant roots and stems.

Age of Wound

In an additional experiment 120 plants of each species were tested to determine the importance of wound age on infection. Two weeks after potting, the plants were gently removed from the potting medium and V-shaped wounds were made on each plant approximately 5.0 cm below the soil line on all plants. Fifteen plants were inoculated with a mycelial disc immediately after wounding and the wounds were covered with vinyl grafting tape. All other wounds were wrapped with vinyl grafting tape and the wounded plants replaced in perlite. At intervals of 1, 2, 4, 8, 16, and 32 days, 15 plants were removed from the potting mixture, inoculated at the wound site, rewrapped with grafting tape, and planted back in perlite. Thirty days after each inoculation date, the plants were removed from the pots and isolations were made from the roots and stems of each plant.

RESULTS

Type of Wound

No infection occurred on unwounded roots. Root wounds were a prerequisite for fungus entry into the plant (Table 1). Any disruption of the periderm on the older roots which allowed the fungus to by-pass these tissues was suitable to fungal entry. The percentages of infection for abrasive, puncture, and vascular wounds were 75, 80, and 85 respectively on redbud, and 50, 55, and 80 on sugar maple. The most efficient wound on both hosts was a vascular wound which placed the pathogen in direct contact with the vessel members.

Age of Wound

Root wounds remained as infection courts up to 32 days on redbud and 16 days on sugar maple seedlings (Table 2). As the age of the wound increased the number of plants infected through wounds decreased. Only 13 percent of the redbud plants became infected when inoculated at wound sites that were 32 days old and no infection occurred through wound sites 32 days old on sugar maple.

Thirty two-day-old wounds had several layers of dead cells which were oc-

cluded with heavily pigmented materials. This condition was a barrier against penetration by the fungus. Many vessel members adjacent to wounds were occluded with tyloses and wound reaction materials. Callus was beginning to form at the margins of the wound after 32 days.

Wounds were not made on other areas of the root. Therefore, location of the wounds may have some significance because wounds made on older secondary tissue may require a longer time for initiation of repair tissue. Younger tissue, i.e., at the root tip or lateral roots, may heal faster and reduce the time a wound remains as an infection court.

DISCUSSION AND CONCLUSIONS

The periderm consists of the phellogen, phellem, and phelloderm which completely surrounds the vascular cylinder of woody plant roots. The cells of the phellogen are parenchyma and remain alive and active. The cells of the phellem become suberized, which renders them virtually waterproof, and at maturity they die, forming a rather impervious, protective layer around the outside of the root.

The fungus gains entrance through

Table 1.—The effect of root wounds on number of redbud and sugar maple plants infected with *Verticillium albo-atrum*.

Type of Wound ^a	Number of Plants Infected		
	Roots Only	Roots and Stems	Total
<i>Redbud</i> — 2 years old			
No wounds	0	0	0
Abrasion	10	5	15
Puncture	9	7	16
Vascular incision	12	5	17
Noninoculated (controls)	0	0	0
<i>Sugar maple</i> — 2 years old			
No wounds	0	0	0
Abrasion	6	4	10
Puncture	8	3	11
Vascular incision	11	5	16
Noninoculated (controls)	0	0	0

^a Twenty plants were used per treatment.

Table 2.—The effect of age of root wounds prior to inoculation with *Verticillium albo-atrum*.

Age of Wound at Inoculation*	Number of Plants Infected
Redbud — 2 years old	
Immediate	10
1 day	8
2 days	7
4 days	4
8 days	3
16 days	2
32 days	2
Noninoculated (controls)	0
Sugar maple — 2 years old	
Immediate	11
1 day	10
2 days	6
4 days	3
8 days	3
16 days	1
32 days	0
Noninoculated (controls)	0

* Fifteen plants were used for each treatment.

root wounds into the vascular system while by-passing the periderm. Any injury acts as an infection court but a wound deep into the stele places the fungus in direct contact with the vessel, thus the infection court is more conducive for penetration by the fungus. Moisture and temperature optima may interact with age of wounds for maximum infection.

The older the wound the less chance for infection by the fungus. This may be correlated with growth responses by the plant at the wound site. Following wounding, a layer of dried cells forms on the pruned surface. These cells die as the result of injury by the knife. Adjacent to the dead cells is a zone which becomes infiltrated with wound substances. The tracheids remain intact and ultimately become occluded with wound substances. Tyloses develop in vessel members adjacent to the wound site. This growth response results in a barrier that prevents the fungus from invading the functional vessel members. The sequence of wound healing may take place much

faster on young root tissue. Vigor of the host plant will affect the time in which root wounds heal over.

Good cultural practices should be followed when planting susceptible hosts in soil that may be infested with *V. albo-atrum*. When digging plant material, care should be taken to keep wounds to a minimum. Digging a ball larger than normal may decrease the chances of severing large roots. Root pruning should be avoided. After planting, the application of fertilizer and water will decrease transplanting shock and increase plant vigor. If the vigor of the plant can be increased, root wounds will heal more quickly and this will decrease the chances of infection.

PENETRATION AND DEVELOPMENT OF *V. ALBO-ATRUM* IN ROOTS OF WOODY HOSTS

MATERIALS AND METHODS

Redbud and green ash [*Fraxinus pennsylvanica* Marsh. var. *subintegerrima* (Vahl.) Fern.] are hereafter designated as susceptible, and honey locust (*Gleditsia triacanthos* L.) and sycamore (*Platanus occidentalis* L.) are hereafter designated as resistant. The susceptible species were selected from a list of susceptible hosts of *Verticillium albo-atrum* as reported by Himelick (1969). The resistant hosts were so designated from unpublished work of E. B. Himelick (personal communication). Isolates 3 and 4 were used to inoculate redbud and green ash respectively. A mixture of Isolates 1, 2, 3, and 4 was used to inoculate honey locust and sycamore. The soil used in the greenhouse was a 1:1:1 ratio by volume of loam soil, peat, and river sand, steamed for 4 hours at 100 C.

To obtain seedlings, seeds were collected in early fall and cold-stratified in sand for 90 days at 5 C. The stratified seeds were immersed for 2 minutes in a 10 percent sodium hypochlorite

solution and germinated in perlite under glass. Twenty seedlings of each species in the 2-leaf stage were inoculated by dipping the roots into an approximate 1×10^4 /ml conidial density of *V. albo-atrum*, by placing 3-mm blocks of PDA containing the fungus on selected areas, and by placing a *Verticillium*-infested oat seed adjacent to a selected area. After inoculation, the seedlings were placed horizontally in 150-mm petri dishes containing sterile peat moss or planted in sterile soil in pots in the greenhouse.

Selected seedlings were sectioned for microscopic examination at intervals after inoculation. The seedlings were removed from the petri dishes or soil and the portions to be sectioned were killed and fixed in FAA, dehydrated in tertiary butyl alcohol, embedded in

paraffin, and sectioned at 12 to 15μ using the technique described by Johansen (1940). The sections were stained with thionin in phenol and counterstained with orange G. in absolute alcohol (Stoughton 1930), then examined under the microscope.

RESULTS

Fungus Growth on Root Surface

The four genera of hosts used were essentially alike morphologically and no differences were detected in the way the fungus penetrated them (Table 3).

The fungus colonized the exterior surface of the epidermis (Fig. 1). The fungal growth was appressed over the entire epidermal surface with conidiphores arising at right angles from the surface. Tissue around the area of penetration became necrotic. Brown

Table 3.—Root colonization of susceptible redbud and green ash, and of resistant honey locust and sycamore seedlings, with *Verticillium albo-atrum*.

		Intensity of Colonization ^a in Susceptible and Resistant Plants in Specified Regions of Penetration					
Days Exposure to Inoculum	Host	Root Tip	Epidermis	Outer Cortex	Inner Cortex	Xylem	Phloem ^b
1	Redbud	3	3	0	0	0	0
	Green ash	3	3	0	0	0	0
	Honey locust	3	2	0	0	0	0
	Sycamore	3	2	0	0	0	0
2	Redbud	3	3	2	1	0	0
	Green ash	3	3	2	1	0	0
	Honey locust	3	3	2	1	0	0
	Sycamore	3	3	2	1	0	0
4	Redbud	3	3	3	2	1	0
	Green ash	3	3	3	2	1	0
	Honey locust	3	3	3	2	0	0
	Sycamore	3	3	3	2	0	0
6	Redbud	3	3	3	3	2	0
	Green ash	3	3	3	3	2	0
	Honey locust	3	3	3	3	1	0
	Sycamore	3	3	3	3	1	0
8	Redbud	3	3	3	3	3	0
	Green ash	3	3	3	3	3	0
	Honey locust	3	3	3	3	1	0
	Sycamore	3	3	3	3	1	0

^a Symbols shown represent infection intensity as follows: 0 = no colonization; 1 = slight colonization; 2 = moderate colonization; and 3 = severe colonization.

^b Passage of the fungus through the phloem into the vessel members occurred but no phloem colonization occurred.

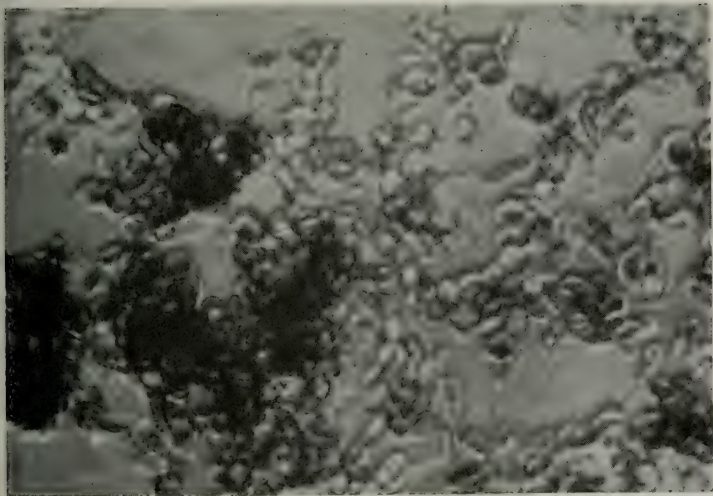


Fig. 1.—*Verticillium* microsclerotia completely colonizing the exterior surface of a green ash root (X 250).

necrotic flecks could be seen extending above but not below the point of infection.

Root Tip Penetration

The fungus penetrated the root cap within 48 hours. The hyphae penetrated both intercellularly and intracellularly, but intracellular penetration was most common. There was no tendency for the cells to separate, which might have occurred if a weakening of the middle lamella took place, unless an extremely high inoculum potential occurred on the root surface.

In the region of root elongation and maturation, the fungus penetrated through the epidermis. Penetration was either direct through the cell wall or between the epidermal cells. The hyphae or germ tubes produced appressorium-like swellings over the epidermis within 48 hours. A penetration peg developed from the appressorium and was smaller in diameter than the parent hypha.

Penetration in Root Hair Region

In the epidermal area between the root hairs, the fungus penetrated at random, both inter- and intracellularly. Germ tubes developed over the root hairs but none was seen penetrating the root hairs. The base of the root hair frequently was penetrated but no further growth occurred.

Penetration in Area of Lateral Root Formation

Another avenue for fungus penetration into roots is the area of lateral root formation. Rupture of the primary root tissue did not occur until the lateral root primordia were well developed. The fungus penetrated the torn areas where the lateral root emerged. Mycelia could be seen in the cortical layers of the lateral root but none was observed in the xylem. At this point in the process of invasion no differences were detected between the susceptible and resistant hosts.

Cortical Invasion — Susceptible Hosts

Most mycelial growth in the cortex was intracellular. Mass penetration resulted from a high inoculum potential at the invading point, and the mycelial development was centripetal (Fig. 2). Many hyphae at the point of penetration formed appressorium-like swellings against the cortical cell wall and penetrated to the next cell layer (Fig. 3a). Other hyphae that penetrated the cortical cells were constricted in diameter at the point of penetration (Fig. 3b).

When the invasion of the inner cortical layers was limited to a few hyphae, no marked centripetal alignment of hyphal strands occurred. Hyphal strands sometimes deviated from the centripetal development and developed tangentially and intercellularly for several cell layers and then penetrated directly through the wall.

Cortical Invasion — Resistant Hosts

Most mycelial growth in the cortex was intracellular. The mycelium was hyaline but became heavily pigmented after 3 days. After 8 days, most hyphae were dark brown, regularly septate, and swollen between the septa so as to appear torulose. These hyphal strands gave rise to microsclerotia by repeated budding (Fig. 4a). Microsclerotia varied in shape, from elongate to irregularly spherical, and varied in size, from 15 to 75 μ in diameter. These microsclerotia continued to enlarge, which caused cortical cells to be separated or expanded many times their normal size (Fig. 4b).

Penetration of Vascular Region of Susceptible Hosts

If the fungus penetrated the cortical cells of the susceptible hosts, it in-

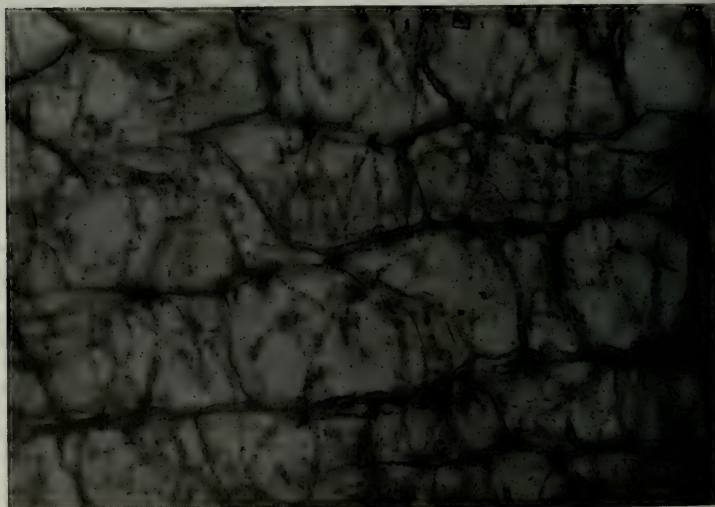


Fig. 2.—Longitudinal section of redbud cortex showing mass penetration of cortical cells resulting from a high inoculum potential at the invasion point (X 400).

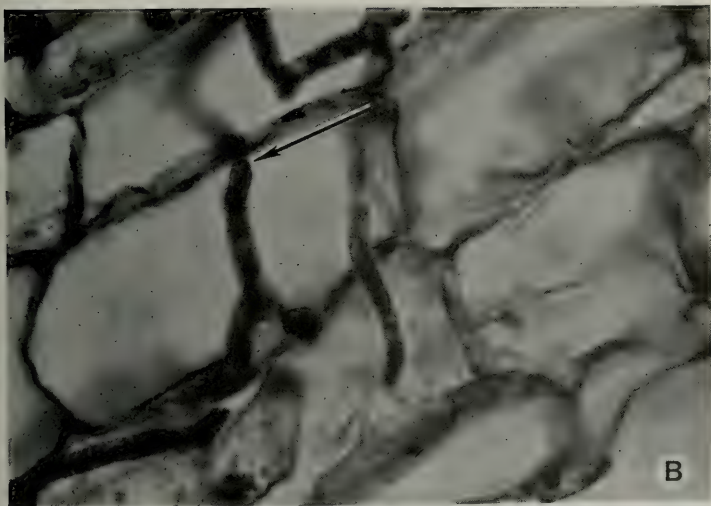
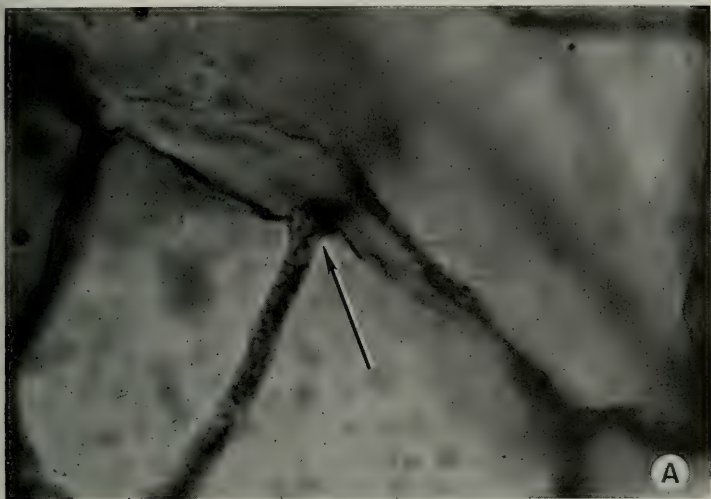


Fig. 3.—Cortical cells in longitudinal section. A) Appressorium-like swellings against the cortical cell wall (X 2500). B) Hyphal constriction in diameter at the point of penetration through a cortical cell wall (X 2000).

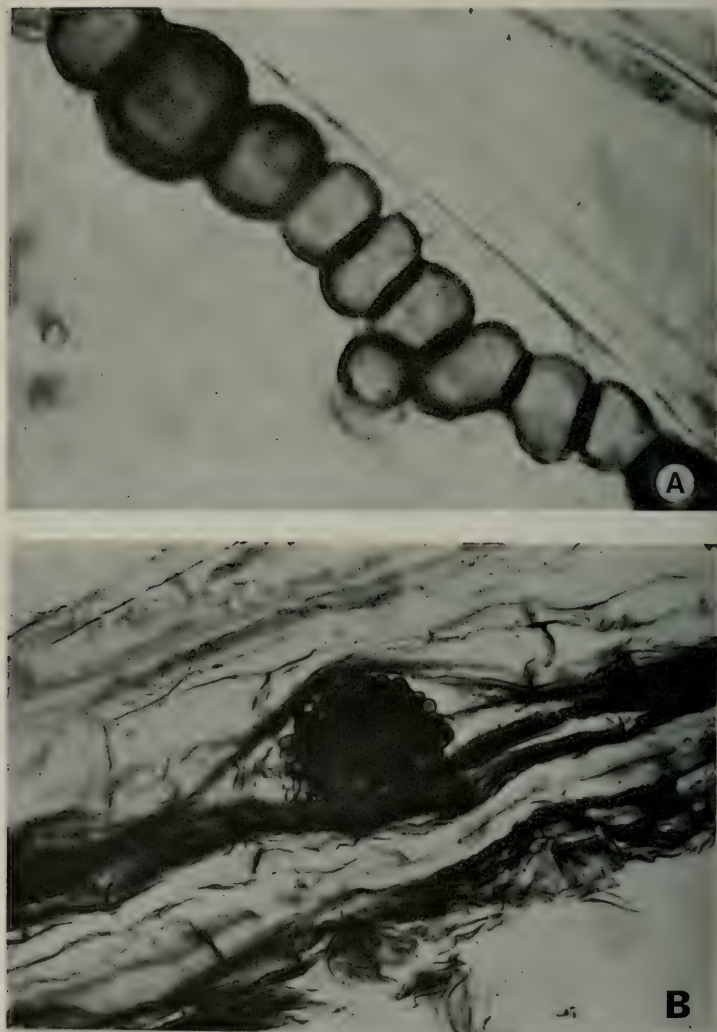


Fig. 4.—Cortical cells of honey locust in longitudinal section. A) Dark brown, septate, budding hypha (X 2200). B) Microsclerotia causing cortical cells to be separated or expanded many times their normal size (X 250).

variably penetrated the endodermis and vessel members. The fungus grew to the endodermal layer within 4 days. The quantity of vessel members invaded appeared related to the number of points of entry and to the mass of mycelia that developed from the points of entry.

The hyphae that penetrated the endodermis usually penetrated the vessel members through pits. The hypha narrowed to a thin, peg-like projection as it grew through the pit. Hyphae did not necessarily stop at the first vessel member contacted, but in many instances they grew out through a pit on the wall of the vessel into an adjacent vessel on the side opposite the entry point (Fig. 5). The mycelium was generally unbranched, hyaline, 3.5μ in width. No typical conidiophores were observed.

Verticillium conidia were observed in the xylem 8 days after inoculation. In most cases, the conidia appeared to be free-floating in the xylem stream and in no way connected with the mycelium present (Fig. 6 and 7). The conidia often were found lodged at the end walls of the vessel members (Fig. 8). No defense mechanism such as tyloses or gum deposits was observed in the xylem members. The lack of a defense mechanism on susceptible hosts is in complete disagreement with other workers' data on hops and cotton (Table 4).

Penetration of Vascular Region of Resistant Hosts

Although the fungus penetrated the cortical cells, few hyphae penetrated the endodermis and vessel members. The quantity of vessel members in-

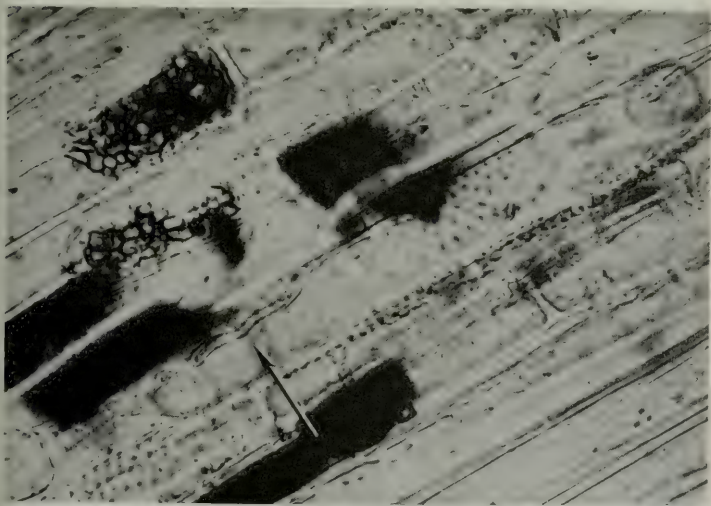


Fig. 5.—Longitudinal section through the vascular cylinder of redbud showing a hypha within a vessel member (X 850).



Fig. 6.—Free-floating conidia of *V. albo-atrum* in a vessel member of green ash (X 500).

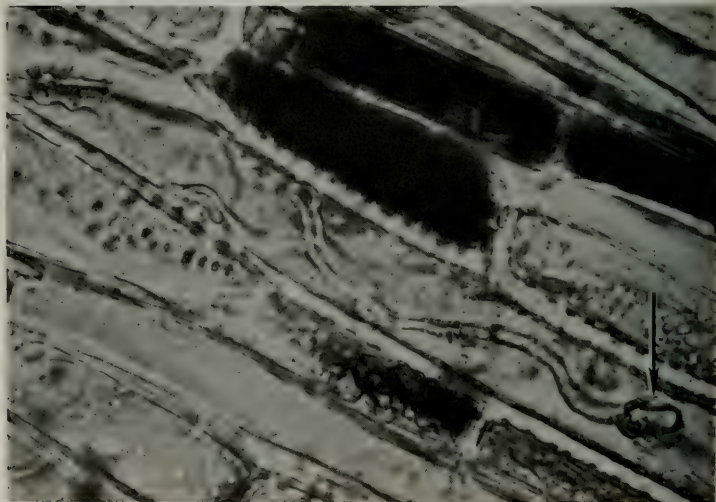


Fig. 7.—Longitudinal section through a vessel member of a redbud root showing a *V. albo-atrum* conidium germinating (X 1700).

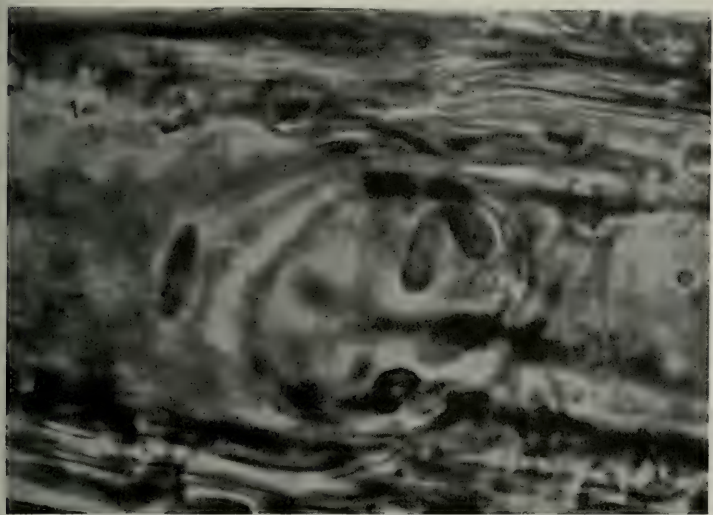


Fig. 8.—Longitudinal section showing lodged conidia at the end walls of the vessel member of a redbud root (X 2300).

Table 4.—A comparison of penetration and development of *Verticillium albo-atrum* in roots of herbaceous and woody hosts.

Region of Infection and Signs of Disease	Intensity of Colonization in Susceptible (S) and Resistant (R) Plants ^a							
	Hops ^b		Cotton ^b		Woody Ornamentals ^c			
	S	R	S	R	S	S	R	R
	Fruggle	OR/55	Daltapine 15	Acata 4-42	Redbud	Green Ash	Honey Locust	Sycamore
Epidermis	3	3	3	3	3	3	3	3
Root hairs	2	2	2	2	0	0	0	0
Lateral roots	0	0	0	0	1	1	1	1
Cortical colonization	3	3	3	3	3	3	3	3
Endodermis	3	3	3	3	3	3	1	1
Phloem colonization	0	0	0	0	0	0	0	0
Xylem colonization	3	2	3	2	3	3	1	1
Conidia (xylem)	3	1	3	2	3	3	0	0
Microsclerotia (cortex)	0	0	0	0	0	0	3	3
Mechanical plugging (xylem)	1	2	2	2	0	0	1	1

^a Symbols shown represent infection intensity as follows: 0 = no colonization; 1 = slight colonization; 2 = moderate colonization; and 3 = massive colonization.
^b Data on hops from Talboys (1958); data on cotton from Garber & Houston (1966).
^c Redbud and green ash are susceptible; honey locust and sycamore are resistant.

vaded did not appear related to the number of points of entry or to the mass of mycelia that developed from the points of entry.

The hyphae that penetrated the endodermis and vessel members did so through pits in the same manner as in the susceptible hosts. Few hyphae

were observed in the vessel members. The mycelium was hyaline, unbranched, and 2.7μ in diameter. The mycelia did not ramify throughout the vessel members as they did in the susceptible hosts. No conidia could be seen in the xylem members although mycelium was present.

Frequently, microsclerotia developed in the vessel members, completely plugging the vessel members (Fig. 9a). They arose from single hyphae by repeated budding of heavily pigmented, thick-walled cells. The microsclerotial cells often grew through pit pairs and moved into adjacent vessel members where repeated budding took place (Fig. 9b and 9c). Germinated microsclerotial cells were also observed that grew through pit pairs into adjacent vessel members.

The ray parenchyma was heavily colonized with microsclerotia. Germ tubes from microsclerotia grew from one parenchyma cell to another through pit pairs or plasmodesmata (Fig. 9d). This may be an avenue for lateral growth of the fungus outward from the central vascular cylinder.

DISCUSSION AND CONCLUSIONS

Conidia of *V. albo-atrum* germinated on the surface of both the susceptible and resistant roots and grew in random directions. Some germ tubes grew away from the host; others penetrated the epidermis. Although germ tube penetration occurred, most epidermal penetration was by either hyphae or germinated microsclerotia. Intercellular and intracellular penetration occurred within 48 hours after inoculation. Nelson (1950) found that *V. albo-atrum* penetrated peppermint roots 6 hours after inoculation. Reid (1958) reported intercellular penetration but observed no intracellular penetration of melon roots by *F. bulbigenum* Cook and Massee.

According to Anderson & Walker (1935), *F. conglutinans* Wollenw. pen-

etrated the cell walls of cabbage plants by mechanical pressure. Talboys (1958) found that the splitting apart of hop cells by *V. albo-atrum* was a mechanical rather than an enzymatic process. My evidence through visual observation did not suggest that an enzyme was involved in either epidermal penetration or cortical invasion unless the cells were invaded by a mass of hyphae. This is in agreement with Garber & Houston (1966) on *Verticillium* invasion of cotton. Direct penetration was either by constriction of a hypha as it passed through the wall or by a peg-like projection of an appressorium-like swelling. Garber & Houston (1966) noted similar structures in cotton cells invaded by *Verticillium*.

I did not observe penetration of root hairs although it has been reported by Smith & Walker (1930) for *Fusarium* invasion of cabbage roots and by Garber & Houston (1966) for *Verticillium* invasion of cotton roots.

The areas of lateral root emergence were not important as infection courts. The fungus penetrated the lateral root and ramified throughout the cortical tissue, but no mycelia were found invading the vascular tissues. Many uninjured roots were invaded to the same cortical layers. Smith & Walker (1930) reported similar observations; however, Reid (1958) suggested that penetration of emerging lateral roots might provide a mechanism for a vascular pathogen to avoid the penetration barrier of the endodermis.

The progress of infection in the susceptible green ash and redbud and the resistant honey locust and sycamore was identical after the point of cortical colonization. The species were alike in morphology and were penetrated by the fungus in a comparable fashion. Differences in fungus growth were noted immediately as the fungus progressed beyond the initial cortical colonization.

In the susceptible species, mycelia

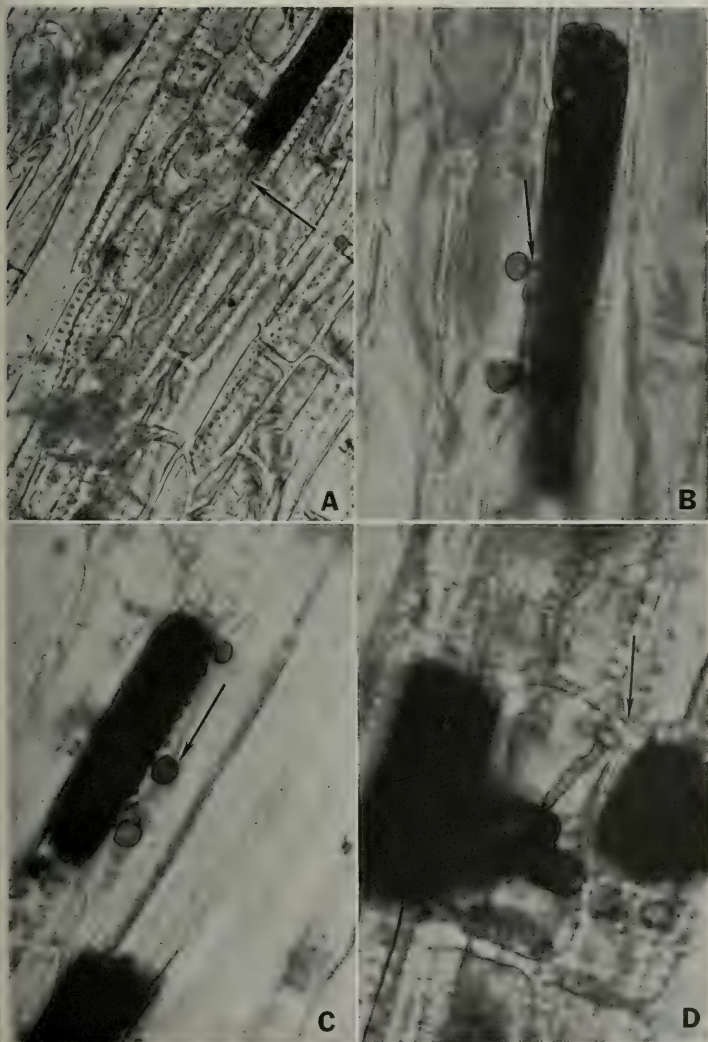


Fig. 9.—Longitudinal section through the vascular cylinder of a sycamore root. A) Germinating microsclerotium of *V. albo-atrum* which has completely plugged a vessel member (X 550). B, C) Budding cells growing through pit pairs into adjacent vessel members (X 1000). D) Ray parenchyma heavily colonized with microsclerotia and microscletum germinating (X 1000).

ramified throughout the tissues and reached the endodermis and xylem elements within 4 days. Conidia were found in the vessels of roots 8 days after inoculation. Lack of mycelial connections between fungus parts present in the xylem and conidia at secondary sites higher in the root system can be explained by conidial movement. It is reasonable to assume that free-floating conidia moved to secondary infection sites and provided for rapid fungus dispersal throughout the plant. In some susceptible cotton plants Schnathorst et al. (1967) found that 30,000 conidia/ml of tracheal fluid were present 96 hours after inoculation.

In the resistant species, microsclerotia were produced in abundance in the cortex. These structures enlarged by repeated budding and ruptured the walls of the cortical cells. Few hyphae penetrated the endodermis and reached the xylem members. Few hyphae were found in the xylem members and conidia were not observed. Schnathorst et al. (1967) found that tolerant varieties of cotton depressed conidial numbers more than 20 fold.

Talboys (1964) postulated that the xylem defense-response is much the same in different species and cultivars of plants. Since it is a generalized response to physical damage and infection, the difference in host resistance to vascular infection is constituted by a difference in response of the extra-vascular tissue at the early stage of infection. This I found to be only partially true. The endodermis prohibited mycelial penetration to some extent in the resistant hosts. However, a xylem-defense response took place after penetration of the vessel members. Few hyphae were found in the vessel members after penetration and no conidial production occurred. Beckman et al. (1962) inoculated bananas with *Fusarium* by means of a standard dose of microconidia introduced into the xylem elements and found a highly sig-

nificant difference between the xylem-defense response of the resistant Lacatan and susceptible Gros Michel bananas. Therefore, Talboys' postulate should be expanded to include the infection sequence in the vascular system in trees.

EFFECT OF ROOT INFECTION ON GROWTH RESPONSE OF REDBUD & GREEN ASH SEEDLINGS

MATERIALS AND METHODS

Redbud and green ash seeds were collected and germinated as previously described. After 3 weeks, 80 seedlings of each species were removed from the germination beds and the roots dipped in inoculum for 5 minutes. After root-dipping, 5 plants were planted in each of 32 No. 10 potting cans.

Isolates 3 and 4 were used to inoculate redbud and green ash respectively. Each isolate was grown on PDA for 14 days at 24 C. The fungus and agar were macerated with water in a Waring blender to produce a thick suspension of inoculum. An equal number of control plants were root-dipped in a PDA blended suspension which did not contain the fungus and potted as described above.

The plants were inoculated on March 29. The first samples of healthy and infected plants were taken on April 12 and at 2-week intervals thereafter until July 19. Ten plants per treatment were sampled on eight occasions making a total of 160 redbud and 160 green ash plants. The following data were obtained from each treatment: stem height, leaf area, total number of leaves produced, fresh and dry weights, water content of leaves, and nitrogen content of stems, leaves, and roots.

Dry weights were obtained by drying the plant parts in an electric oven at 80 C for 72 hours. Leaf areas were determined by weighing a specific

known leaf area as compared to the weight of the whole leaf.

Micro-Kjeldahl determinations for total nitrogen were made on bulk samples of leaves, stems, and roots from healthy and infected plants.

All data for stem height, leaf area, and dry weight were analyzed statistically using a one-way analysis of variance and student "T" tests.

RESULTS

Symptoms

Fourteen days after inoculation, young inoculated plants were retarded in growth but no wilt symptoms were apparent. Two weeks later the plants were stunted and the leaves had failed to expand.

Sectioned roots and stems showed extensive invasion of the vessel members by the fungus. The hyphae were confined to the primary xylem vessel members 16 weeks after inoculation.

Dry Weight

Infection markedly reduced dry-matter production on both redbud and green ash seedlings. The mean values for the dry weight of whole plants for controls and infected plants are shown in Table 5 and Fig. 10. All weight data for leaves, stems, and roots were analyzed statistically and the mean values for the dry weights on all

sampling periods after inoculation are given in Tables 6 and 7 and Fig. 11 and 12. When comparing healthy and infected plants, a significant difference in dry weight was evident for leaves and stems of redbud and leaves of green ash 14 days after inoculation. A significant difference in dry weight of roots of both hosts occurred 28 days after inoculation. On July 19, 112 days after inoculation, the percentage differences for healthy and infected plants were 45, 53, and 47 for leaves, stems, and roots of redbud, and 36, 17, and 24 for leaves, stems, and roots of green ash, respectively.

Leaf Number

The mean values for the number of leaves for healthy and infected redbud and green ash plants are given in Table 8 and Fig. 13. The infected plants showed limited leaf production 28 days after inoculation, and thereafter the rate of leaf production differed little in the two groups.

Stem Height

The mean values for stem height of healthy and infected redbud and green ash plants are given in Table 9 and Fig. 14. A significant difference in stem height of redbud and green ash was not evident until 42 days and 28 days after inoculation, respectively. The initial reduction in growth due to infection

Table 5.—The dry weight of redbud and green ash seedlings infected with *Verticillium albo-atrum*.

Days After Inoculation	Mean Dry Weight (g per plant) ^a (10 Plants)			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
14	.23	.16*	.22	.16*
28	.75	.22**	1.20	.44**
42	.77	.30**	1.49	.50**
56	2.29	.51**	2.87	1.11**
70	3.36	2.20**	3.89	2.13**
84	4.62	2.96**	5.25	3.04**
98	7.12	3.56**	7.23	4.09**
112	8.21	4.29**	10.54	7.20**

^a An asterisk denotes a significant difference (0.05) between noninoculated and inoculated means, and two asterisks denotes a highly significant difference (0.01).

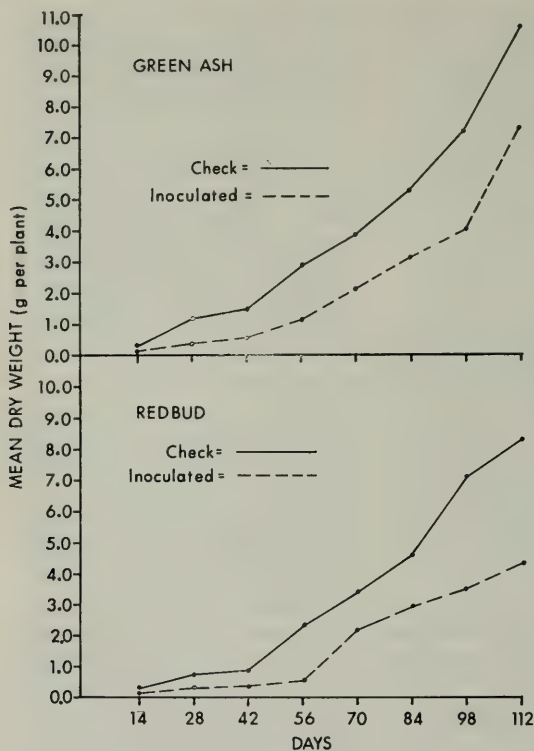


Fig. 10.—The dry weights of green ash and redbud seedlings after inoculation with *V. albo-atrum*.

Table 6.—Dry weights of leaves, stems, and roots of redbud seedlings infected with *Verticillium albo-atrum*.

Days After Inoculation	Mean Dry Weight (g per plant) ^a (10 Plants)					
	Leaves		Stems		Roots	
	Noninoculated	Inoculated	Noninoculated	Inoculated	Noninoculated	Inoculated
14	.11	.06*	.04	.01**	.07	.05
28	.36	.10**	.14	.07**	.11	.07*
42	.82	.13**	.22	.05**	.16	.08**
56	1.02	.25**	.67	.15**	.58	.11**
70	1.61	1.07**	.97	.64**	.82	.49**
84	2.17	1.53**	1.23	.73**	1.16	.69**
98	3.45	1.70**	1.99	.95**	1.68	.90**
112	3.97	2.18**	2.36	1.10**	1.91	1.01**

^a An asterisk denotes a significant difference (0.05) between noninoculated and inoculated means, and two asterisks denotes a highly significant difference (0.01).

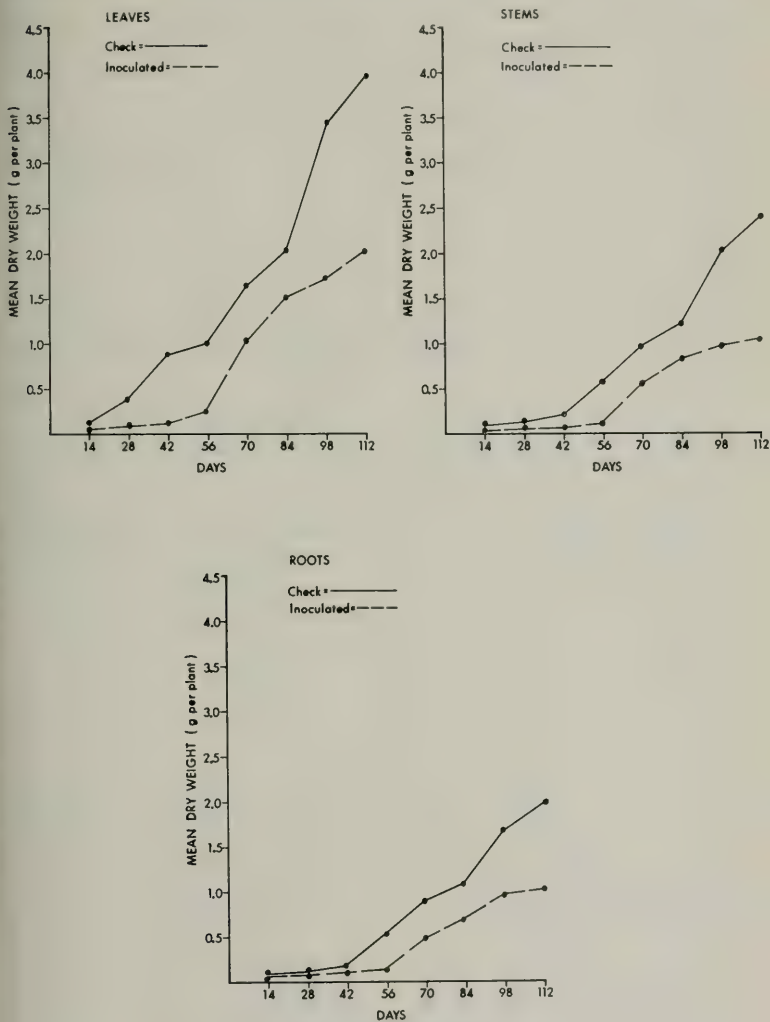


Fig. 11.—The dry weights of leaves, stems, and roots of redbud seedlings after inoculation with *V. albo-atrum*.

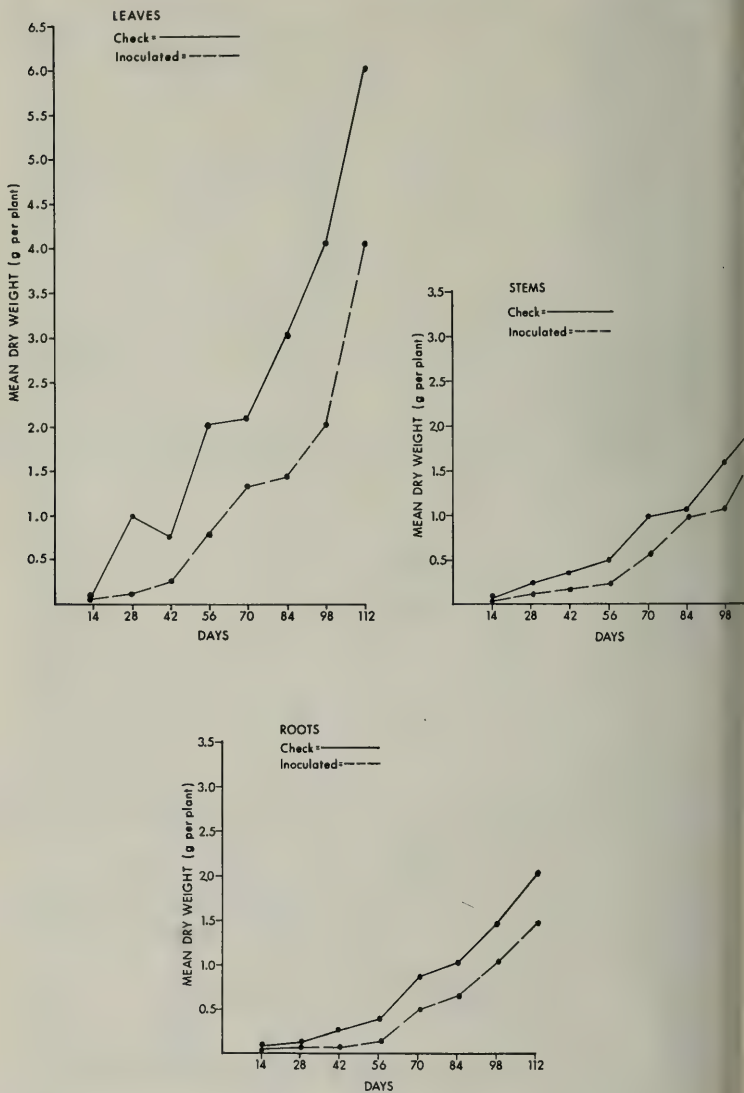


Fig. 12.—The dry weights of leaves, stems, and roots of green ash seedlings after inoculation with *V. albo-atrum*.

Table 7.—Dry weights of leaves, stems, and roots of green ash seedlings infected with *Verticillium albo-atrum*.

Days After Inoculation	Mean Dry Weight (g per plant) ^a (10 Plants)					
	Leaves		Stems		Roots	
	Noninoc- ulated	Inoc- ulated	Noninoc- ulated	Inoc- ulated	Noninoc- ulated	Inoc- ulated
14	.11	.06*	.03	.02	.04	.03
28	1.04	.16**	.21	.11**	.15	.07*
42	.74	.25**	.35	.12**	.25	.07**
56	2.08	.77**	.49	.20**	.35	.14**
70	2.13	1.30**	.90	.56**	.80	.47**
84	3.08	1.43**	1.18	.92**	1.00	.69**
98	4.02	2.05**	1.67	1.08**	1.45	1.04*
112	6.26	4.01**	2.11	1.76**	1.91	1.45**

^a An asterisk denotes a significant difference (0.05) between noninoculated and inoculated means, and two asterisks denotes a highly significant difference (0.01).

Table 8.—Influence of root infection of redbud and green ash seedlings on total number of leaves produced per plant.

Days After Inoculation	Mean Number of Leaves Per Plant (10 Plants)			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
0	3.20	3.50	7.56	7.68
14	4.80	4.02	10.00	8.50
28	7.60	5.37	14.35	10.20
42	8.60	6.20	16.27	12.73
56	10.08	7.48	18.75	14.88
70	10.90	8.65	20.95	16.90
84	12.20	10.06	22.67	19.06
98	13.10	11.30	23.80	20.80
112	14.00	12.20	24.00	22.80

was slight, but further growth of the inoculated plants was reduced. The difference in stem height between healthy and infected plants 112 days after inoculation was 37.5 percent for redbud and 30 percent for green ash.

Nitrogen Content

The nitrogen content percentages of redbud and green ash leaves, stems, and roots of healthy and infected plants are given in Table 10. There was 26 percent less N in infected redbud stems and 31 percent less in infected green ash stems when compared with the controls 112 days after inoculation. The N content in the leaves and roots was

higher in the infected plants than in the healthy controls.

Water Content of Leaves

From the fresh-weight and dry-weight data, the percentage water content of leaves was determined. The leaf data for healthy and infected plants are given in Table 11.

There was no definite pattern of water content between infected and healthy redbud or green ash seedlings. Frequently (but not consistently) the water content of the infected seedlings was above that of the healthy controls. Wilt symptoms did not occur at any time during the experiment. No cor-

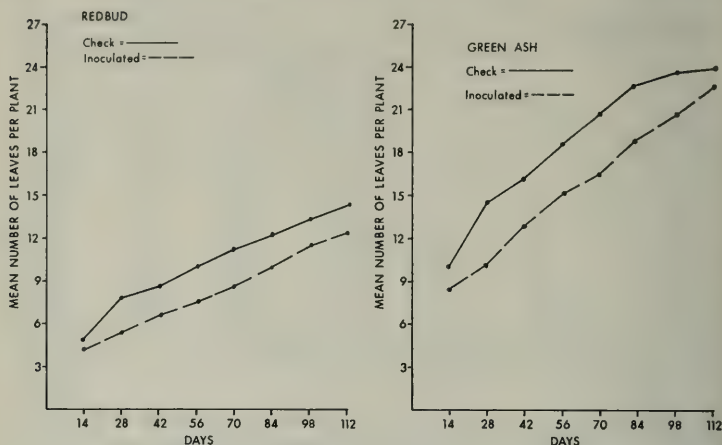


Fig. 13.—Influence of root infection of redbud and green ash seedlings on total number

of leaves produced per plant.

Table 9.—Influence of root infection on stem height of redbud and green ash seedlings.

Days After Inoculation	Mean Stem Height (cm per plant) ^a (10 Plants)			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
0	6.20	6.01	6.31	5.96
14	6.90	6.35	7.58	6.80
28	8.37	7.30	13.45	9.04**
42	9.25	7.51**	15.16	11.58**
56	9.75	7.64**	19.86	13.46**
70	12.00	8.02**	22.53	15.20**
84	13.50	8.70**	25.67	16.83**
98	15.00	9.15**	28.25	18.75**
112	16.00	10.00**	32.00	22.40**

^a An asterisk denotes a significant difference (0.05) between noninoculated and inoculated means, and two asterisks denotes a highly significant difference (0.01).

relation could be made on water content between healthy and infected seedlings due to sampling time or greenhouse watering maintenance

Leaf Area

The mean values for leaf area of redbud and green ash are given in Table 12. A significant difference in leaf area of healthy and infected redbud and green ash was found 14 days

after inoculation. A highly significant difference occurred on both hosts after 28 days. Although leaf area was less in infected plants, deformity of the leaves was not observed.

DISCUSSION AND CONCLUSIONS

The presence of *V. albo-atrum* might be expected to affect the metabolism of the host in any or all of the following ways: a) obstruction to water absorp-

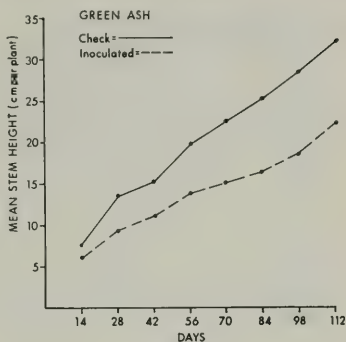
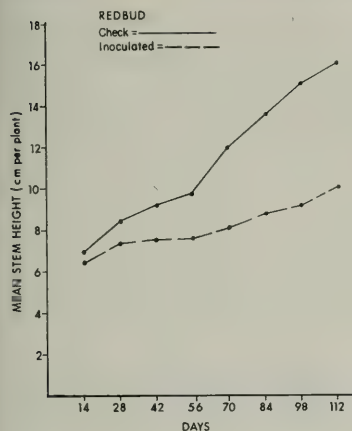


Fig. 14.—Influence of root infection on stem height of redbud and green ash seedlings after inoculation with *V. albo-atrum*.

Table 10.—Influence of root infection on total nitrogen content of leaves, stems, and roots of redbud and green ash seedlings.

Days After Inoculation	Total Nitrogen (percent dry weight)			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
<i>Leaves</i>				
14	2.61	3.26	4.00	3.50
56	2.00	3.63	5.45	4.98
112	2.87	3.41	3.03	4.11
<i>Stems</i>				
14	1.71	1.23	4.50	4.10
56	2.17	1.36	4.34	3.56
112	1.47	1.09	4.04	2.75
<i>Roots</i>				
14	2.13	1.86	3.02	3.31
56	1.64	2.00	2.36	2.50
112	1.50	1.69	2.10	3.95

tion and movement; b) obstruction to the uptake and translocation of mineral nutrients; and c) production of toxic substances. The data have been examined in the light of these hypotheses.

Infection leads to a drastic reduction in dry-matter production of all parts of the plant. The greatest effect of infection was a reduction in stem height and leaf area. Total leaf area decreased significantly in the inoculated plant when compared with the control. The

number of leaves per plant exhibited only a slight initial reduction and thereafter was little affected.

Nitrogen is one of the most important major nutrients affecting leaf expansion, but there was no evidence of a reduction in the uptake of nitrogen. Frequently, the nitrogen content was higher in the infected plants than in the control plants. The results are surprising since the root system is the first part of the plant to be affected by the

Table 11.—The water content of redbud and green ash leaves in response to root infection with *Verticillium albo-atrum*.

Days After Inoculation	Percentage Water Content of Leaves ^a			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
14	70	71	78	75
28	60	73	74	84
42	59	63	78	75
56	52	63	55	62
70	53	50	67	58
84	52	48	60	71
98	52	50	62	70
112	51	54	55	52

^a Percentage water content was calculated from the difference between the dry weight and the fresh weight.

Table 12.—Influence of root infection on leaf area of redbud and green ash seedlings.

Days After Inoculation	Mean Value of Leaf Area Per Plant (cm ²) ^a			
	Redbud		Green Ash	
	Noninoculated	Inoculated	Noninoculated	Inoculated
14	32.62	22.65*	29.84	21.32*
28	72.70	36.21**	63.81	31.37**
42	99.04	40.41**	108.43	65.72**
56	107.54	54.75**	141.01	83.20**
70	138.18	109.64*	186.39	103.21**
84	145.23	129.88*	207.46	136.81**
98	190.31	147.14*	265.78	183.21**
112	203.08	157.86*	298.76	201.21**

^a An asterisk denotes a significant difference (0.05) between noninoculated and inoculated means, and two asterisks denotes a highly significant difference (0.01).

fungus, and thus mineral absorption might be impaired. No other mineral nutrients were determined but it would seem unlikely that infection would interfere with their uptake or translocation.

A low water supply might be expected to account for the general stunting which occurred. However, the water content in this experiment was approximately the same for the infected plants and controls, and there were no symptoms of general wilt.

The results of the growth analysis may be interpreted in terms of a toxin theory. The reduction in growth may be initiated by toxins entering the stems and leaves at concentrations below the level that would cause wilt or death. This could affect cell extension or re-

duce photosynthesis. Therefore, at the meristems the toxins may interfere with stem elongation and thus reduce internode growth. The fact that general wilting was never observed would indicate a greater tolerance of toxin by young plants.

EFFECT OF TEMPERATURE & HEAT TREATING ON DEVELOPMENT OF *V. ALBO-ATRUM* IN ROOTS

MATERIALS AND METHODS

Redbud and green ash seeds were collected and germinated as previously described. At the 2-leaf stage, plants were removed from the germination bed and root-dipped in inoculum for 5 minutes.

Isolates 3 and 4 were used to inoculate redbud and green ash respectively. Each isolate was grown on PDA for 14 days at 24 C. The fungus mycelia and agar were macerated with water in a Waring blender to produce a thick suspension of inoculum. The control plants were root-dipped in a PDA solution without the fungus.

After the roots were dipped, the plants were potted in perlite and allowed to grow for 14 days. The plants were then removed from the perlite and the roots were excised at the ground line.

To study the effects of temperature on microsclerotial development, the excised roots were incubated at continuous temperatures ranging from 5 to 35 C at 5-degree intervals. The roots were wrapped in moist paper towels and then placed in capped bottles to maintain a moist atmosphere.

Cultures of the fungus on PDA were grown at the same range of temperatures. Observations were made on the production of microsclerotia.

The influence of the soil microflora on microsclerotial formation was determined by incubating whole roots in sterile and nonsterile soil in capped bottles. Two soil-moisture levels were used. One level approximated field capacity; the other approximated one-half field capacity. The temperature was maintained at 25 C for the 28-day test.

Both tests had four root systems per treatment replicated three times. Observations were made at 7-day intervals for 35 days. For microscopic observation, roots were cut into small pieces, sectioned on a freezing microtome, and stained in cotton blue.

RESULTS

Effect of Temperature

Abundant microsclerotia were observed in roots after 14 days incubation at 15, 20, 25, and 30 C. Microsclerotia

did not develop at 35 C and were not observed in roots incubated at 5 and 10 C until after 35 days. The microsclerotia tend to develop as compact balls of dark-walled cells (Fig. 15). At the lower temperatures, individual microsclerotia tended to be elongated, and some were reduced to single strands of rounded, dark-walled cells.

Although the fungus failed to form microsclerotia on PDA at 35 C, a limited amount of mycelial growth occurred. After 14 days' growth, abundant microsclerotia were produced (Fig. 16) at 15, 20, 25, and 30 C. Fewer microsclerotia developed at 30 and 10 C. Little growth occurred on PDA after 14 days at 5 C, but measurable hyphal growth occurred after 35 days. Thus, microsclerotial development on PDA closely paralleled development in moistened roots at similar temperatures.

Effect of Heat Treating of Soil

Microsclerotia developed in dead roots incubated in both steamed and nonsteamed soil. Moisture levels near the field capacity of the soil were more favorable for microsclerotial development. Relatively few microsclerotia developed in nonsterile soil at the low moisture level. Although microsclerotia developed uniformly and more abundantly in steamed soil, appreciable numbers of microsclerotia were found in nonsteamed soil.

DISCUSSION AND CONCLUSIONS

The microsclerotia of *V. albo-atrum* develop rapidly at 15 to 30 C in excised green ash and redbud roots after being incubated at high moisture levels. Microsclerotia were produced at 5 C, but a longer incubation period was required. Temperature requirements for microsclerotial development on PDA and in dead host tissue were similar.

The development of microsclerotia at low temperatures is important in inoculum increases in overwintering de-

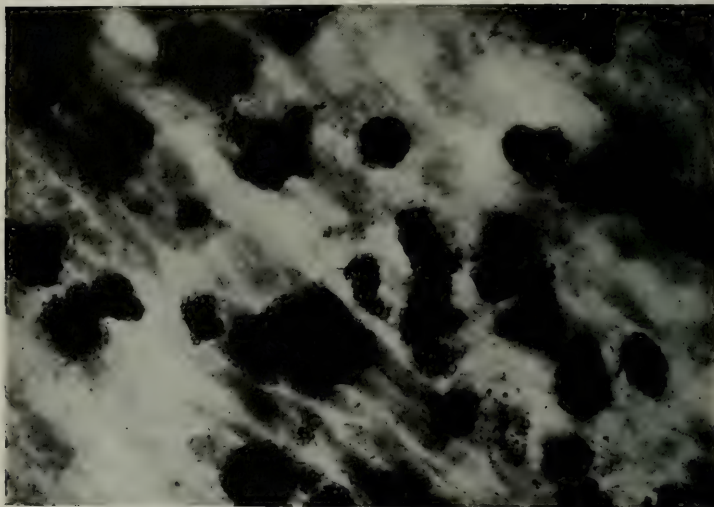


Fig. 15.—*V. albo-atrum* microscerotia consisting of compact balls of dark-walled cells on dead root tissue (X 250).

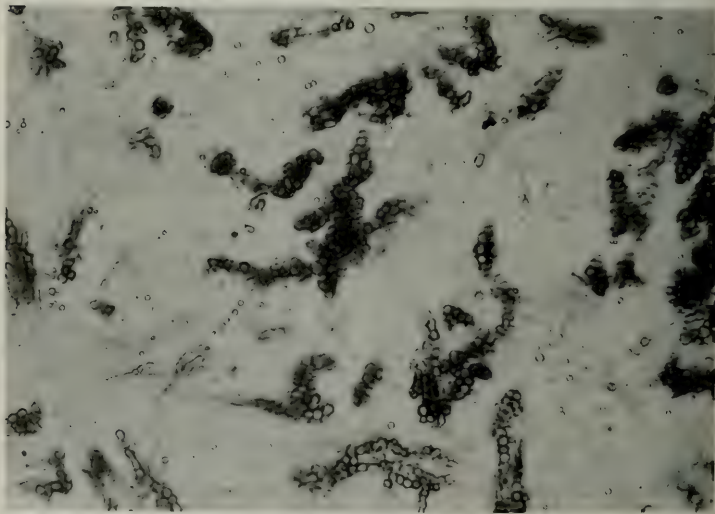


Fig. 16.—*V. albo-atrum* microscerotial development on PDA (X 250).

bris. Evans et al. (1966) found large numbers of microsclerotia in overwintering cotton stalks where fall and winter weather temperatures were relatively low and there was sufficient moisture. The range of temperatures at which microsclerotia form permits the fungus to compete favorably with organisms that decompose root debris. Born (1971) found that heat-treating the soil increases symptom development because of a decrease in competition with other fungi.

The present study indicates that with high temperature and low soil moisture prior to microsclerotial development, the inoculum level was significantly reduced.

EVALUATION OF SYSTEMIC FUNGICIDES AGAINST *V. ALBO-ATRUM*

MATERIALS AND METHODS

V. albo-atrum Isolates 1 and 2 were used throughout this study. Inocula for laboratory studies were prepared by growing the fungus for 14 days at 24 C in petri dishes containing PDA.

Greenhouse experiments were initiated in March and ran through June. The day and nighttime temperatures were approximately 25 and 16 C, respectively. The soil consisted of a mixture of equal parts by volume of loam, peat, and river sand, steamed at 100 C for 4 hours. Soil pH varied from 6.5 to 7.2.

Inocula for infesting soil were produced by growing the fungus for 14 days at 24 C in petri dishes containing PDA. The fungus mats, containing both microsclerotia and conidia, were fragmented in tap water in a Waring blender for 2 minutes. The fungus was added to the soil at the rate of one culture mat in 100 ml of water/20,000 g of soil. The soil was stirred after adding the inoculum to distribute the fungus uniformly throughout the soil. To determine the inoculum potential in the

soil, the soil mixture was air-dried and screened to break up large particles. One-g samples were diluted with sterile water to 10⁶ g/ml, and 1 ml aliquots plated out on PDA + streptomycin. This measured an inoculum potential of 250,000 propagules/g of dry soil.

When plants were inoculated directly, a V-shaped wound was made with a scalpel on the primary root approximately 5 cm below the soil line. A 5-mm mycelial disc was inserted under each flap, pressed in place, and wrapped with vinyl grafting tape to prevent drying of the inoculum and wound area.

The fungicides subjected to laboratory and greenhouse evaluation were: Benlate 50 percent WP [Methyl-1-(butylcarbamoyl) 2-benzimidazolecarbamate]=benomyl; Thiabendazole 60 percent WP [2-4-(thiazolyl) benzimidazole]=TBZ; Bravo-6F 54 percent (tetrachloroisophthalonitrile); and Vitavax 75 percent WP (5, 6-dihydro-2-methyl-1, 4-oxathiin-3-carboxanilide).

Laboratory Studies

The four fungicides were tested in vitro to determine the antifungal activity of each against *V. albo-atrum*. Concentrations of 1,000, 500, 100, and 10 µg/ml (active ingredient) aqueous suspension of each fungicide were prepared and 10-mm Whatman filter discs were soaked for 5 minutes in each concentration. Sterile PDA culture plates were seeded with a conidial suspension and discs from each fungicide were placed on the seeded culture plates, two per plate. This was replicated four times using a factorial arrangement of treatments (4 trials x 4 fungicides x 4 levels) in a completely random design with four plates per treatment combination. Zones of inhibition were measured after 4 or 5 days, at which time growth on control plates had entirely covered the agar surface.

Laboratory bioassays were conducted on plant materials used in fungicide

tests in the greenhouse. The plants were severed at the base of the stem and divided into three regions: (1) terminal, characterized by fully expanded terminal leaves; (2) center; and (3) bottom, located about 5 cm above the severed base of the stem. Leaf discs (9 mm diameter) and wood and bark sections (100 mm long) from each region were frozen at -10°C for 24 hours prior to being placed into petri dishes which contained 15 ml PDA seeded with a conidial suspension of *V. albo-atrum*. After the plates were incubated at 24°C for 7 days, the diameters of the zones of inhibition were measured to determine the relative concentration of fungitoxicant present in the sample.

Greenhouse Studies

SOIL DRENCHES.—Three hundred twenty seedlings each of sugar maple and Russian olive were used as plant material. The seedlings were 2 years old, bare-rooted, and 45–60 cm in height. The seedlings had no previous treatment and were just breaking dormancy. Plants wound inoculated or placed in infested soil were potted 2 weeks prior to fungicide treatment. Control plants were treated identically, but without the fungus. Eight different treatment combinations for each of the four fungicides were tested; with 36-treatment combinations arranged as a $4 \times 3 \times 3$ factorial [four fungicides $\times$ three levels (two rates and a control)] $\times$ three infestations (with and without fungus) in a completely randomized design giving a total of 320 observations per species. The eight treatments were: (1) infested soil, non-treated plants; (2) wound inoculated, nontreated plants; (3) infested soil, plants treated with $1,500\text{ }\mu\text{g/ml}$; (4) infested soil, plants treated with $500\text{ }\mu\text{g/ml}$; (5) wound inoculated, plants treated with $1,500\text{ }\mu\text{g/ml}$; (6) wound inoculated, plants treated with $500\text{ }\mu\text{g/ml}$; (7) noninfested soil, plants treated with $1,500\text{ }\mu\text{g/ml}$; (8) non-

infested soil, plants treated with $500\text{ }\mu\text{g/ml}$. Each plant was placed in a No. 10 potting can. In each pot, 200 ml of the fungicide at the designated concentration were applied as soil drenches three times at weekly intervals. Water was applied and the soil kept moist by watering when required. All fungicide treatments had 10 plants per treatment except that the benomyl treatments had 25 plants per treatment. Disease control was calculated by using the following formula.

$$\text{Percent disease control} = \frac{\text{Disease incidence in control} - \text{Disease incidence in treated}}{\text{Disease incidence in control}} \times 100$$

The noninfested treated pots were used for detection of fungicide phytotoxicity on seedlings.

FOLIAR TREATMENTS.—A benomyl derivative was applied to the foliage of sugar maple and Russian olive seedlings to evaluate its effectiveness as a foliar fungicide. Solutions of the benomyl derivative were prepared as follows: benomyl (5.0 g of active chemical) was dissolved in 100 ml of 85-percent concentrated lactic acid over heat and brought up to a liter with distilled water ($5,000\text{ }\mu\text{g/ml}$); benomyl (5.0 g of a.c.) was dissolved in a liter of distilled water over heat in which 2 ml of concentrated sulfuric acid had been added ($5,000\text{ }\mu\text{g/ml}$); benomyl (5.0 g of a.c.) was suspended in a liter of distilled water ($5,000\text{ }\mu\text{g/ml}$). The pH of the benomyl-lactic acid-water solution was 1.2–1.5, and of the benomyl-sulfuric acid-water solution was 2.5–3.0.

Each formulation of the benomyl derivative was applied to an equal number of plants 2 weeks prior to soil infestation. Another group of plants was treated with each formulation 2 weeks after soil infestation. Foliage was dipped twice to run-off in late afternoon to retain moisture on the foliage as long as possible. The fungicide was

prevented from contaminating the soil by the placing of a cardboard cover on the top of each can before dipping.

To determine if the benomyl derivative could be translocated from the place of application to new growth in sugar maple seedlings, foliar dips were applied to localized areas. A benomyl-lactic acid-water solution was prepared as previously described. Treatments with 5,000 $\mu\text{g/ml}$ were applied in three different ways — to the top three leaves, applied to leaves on the lower two branches, and applied to all leaves on one side of the plant.

The agar diffusion bioassay method was used to detect fungitoxic chemicals in 9-mm leaf discs above and below the area of treatment or in 10-mm sections of xylem tissue.

ROOT TREATMENTS.—Benomyl, thiabendazole, Bravo-6F, and Vitavax were applied as root dips to evaluate each fungicide as a prophylactic against root penetration by the pathogen. Four liters of each fungicide were formulated at 1,500 $\mu\text{g/ml}$ in distilled water. Ten plants of each species were allowed to stand in each fungicide for 5 minutes. Only the roots were covered with the fungicide. After 5 minutes each plant was removed from the dip, shaken to remove excess liquid, and planted in infested soil. Each plant was potted in a No. 10 potting can. Data on phytotoxicity and symptom development were recorded.

RESULTS

Symptoms

Initial wilt symptoms occurred within 7–10 days on both sugar maple and Russian olive seedlings after being inoculated by the wound method. When the plants were placed in infested soil, symptoms occurred within 12 to 14 days. The progression of symptom development was the same regardless of the inoculation method. The leaves rapidly lost their turgidity within 2–3 days. Browning of the leaves and premature leaf drop occurred soon after the leaves had wilted. Unlike larger trees where only a branch or several branches may wilt, these seedlings wilted quickly and completely.

Laboratory Studies

With the paper disc bioassay *in vitro*, benomyl and TBZ were highly inhibitory at a concentration of 10 $\mu\text{g/ml}$ (Table 13). Vitavax was somewhat less fungitoxic, and Bravo-6F was much less active. As the concentration of each fungicide decreased the zone of inhibition decreased proportionately (Fig. 17). The minimum concentration of benomyl and TBZ that inhibited growth was 0.01 and 0.1 $\mu\text{g/ml}$, respectively. The minimum concentration of Vitavax was 0.1 $\mu\text{g/ml}$ and for Bravo-6F it was 1 $\mu\text{g/ml}$.

In PDA plates containing benomyl or TBZ, conidia germinated but failed to grow more than a few microns in

Table 13.—Paper disc bioassay of fungicides against *Verticillium albo-atrum* *in vitro*.

Concentration ^a $\mu\text{g/ml}$	Fungicide			
	Benomyl	Thiabendazole	Bravo-6F	Vitavax
	Diameter of zone of inhibition (mm) ^b			
1000.000	48	55	12	47
500.000	41	53	8	41
100.000	30	43	6	18
10.000	25	39	5	15
1.000	11	8	1	7
0.100	3	1	..	2
0.001	1	..	..	..

^a $\mu\text{g/ml}$ based on weight of active ingredient of fungicide.

^b Zone of inhibition computed as average of four trials with four replications per trial.

length. When single conidia were transferred from these plates to PDA slants after 10 days, more than 90 percent gave rise to established colonies.

Greenhouse Studies

SOIL DRENCHES.—When benomyl, TBZ, Vitavax, and Bravo-6F were ap-

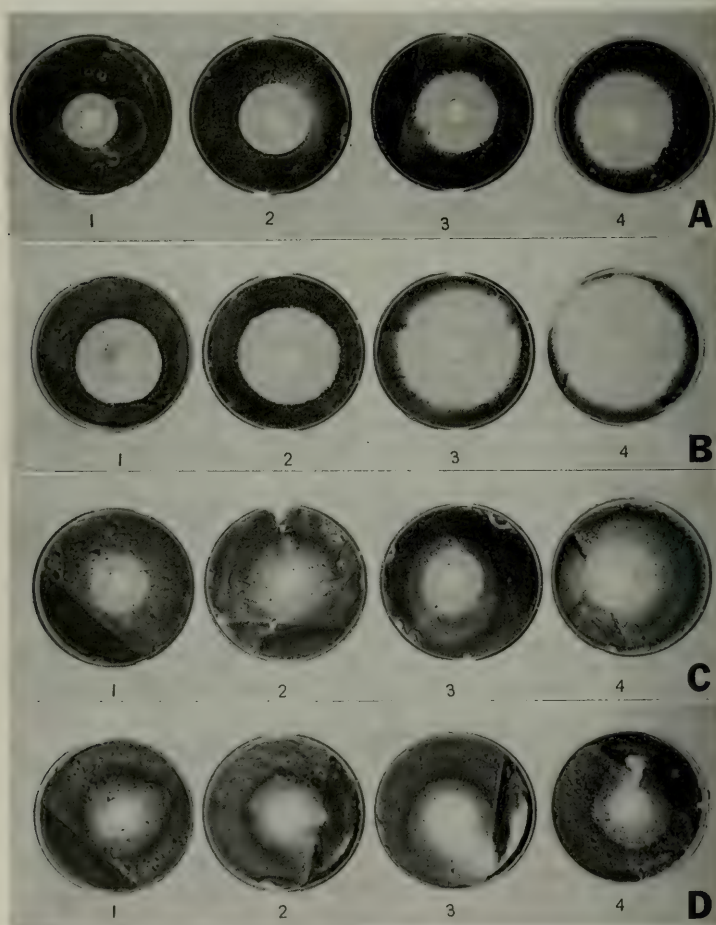


Fig. 17.—Filter paper disc bioassay of four fungicides for the control of *V. albo-atrum* illustrating zones of inhibition outward from filter discs. A) Benomyl. B) Thiabendazole. C) Bravo-6F. D) Vitavax (1 = 10 $\mu\text{g/ml}$; 2 = 100 $\mu\text{g/ml}$; 3 = 500 $\mu\text{g/ml}$; 4 = 1,000 $\mu\text{g/ml}$).

plied as soil drenches to sugar maple and Russian olive seedlings, each gave some degree of disease control except Bravo-6F at 500 $\mu\text{g/ml}$ (Table 14). Benomyl, TBZ, Vitavax, and Bravo-6F, in descending order, were effective when applied 2 weeks after soil infestation. Benomyl at 1,500 $\mu\text{g/ml}$ gave the best control of Verticillium wilt of both sugar maple and Russian olive seedlings. The fungicide concentration, whether at 1,500 $\mu\text{g/ml}$ or 500 $\mu\text{g/ml}$, at the time of application made little difference in the percentage of disease control. Benomyl at 1,500 $\mu\text{g/ml}$ and 500 $\mu\text{g/ml}$ gave 47.5 and 42.5 percent

disease control, respectively, on sugar maple seedlings. Differences were noticed when comparisons were made between fungicides and fungicide concentrations. On Russian olive seedlings, TBZ at 500 $\mu\text{g/ml}$ gave the same amount of control as Vitavax at 1,500 $\mu\text{g/ml}$. Benomyl at 500 $\mu\text{g/ml}$ gave less control than TBZ at 1,500 $\mu\text{g/ml}$. Therefore the rate of soil application of any one fungicide is important in the control of the disease.

Bioassay of terminal, center, and lower leaves of plants treated with a soil drench with each fungicide showed the highest accumulation of the fungi-

Table 14.—Effect of soil drenches for the control of Verticillium wilt of sugar maple and Russian olive seedlings.

Fungicide and Concentration ^a	Number of Plants	Intensity of Infection ^b		
		Plants With Wilt Symptoms	Plants Without Wilt Symptoms	Percent Disease Control
<i>Sugar maple</i>				
Benomyl				
1,500	50	21	29	47.5
500	50	23	27	42.5
Thiabendazole				
1,500	20	10	10	37.5
500	20	11	9	31.2
Bravo-6F				
1,500	20	15	5	6.3
500	20	16	4	0.0
Vitavax				
1,500	20	12	8	25.0
500	20	14	6	12.0
Control	20	16	4	0.0
<i>Russian olive</i>				
Benomyl				
1,500	50	19	31	55.0
500	50	24	26	43.5
Thiabendazole				
1,500	20	9	11	47.0
500	20	10	10	41.1
Bravo-6F				
1,500	20	15	5	12.0
500	20	17	3	0.0
Vitavax				
1,500	20	10	10	41.1
500	20	11	9	35.3
Control	20	17	3	0.0

^a Fungicides applied three times as a soil drench at the rate of 200 ml of aqueous suspension per pot. Plants bioassayed 30 days after last treatment. Concentration at $\mu\text{g/ml}$ active ingredient-aqueous suspension.

^b Data on symptom development taken 30 days after last treatment.

toxicant in the lower leaves and stems (Tables 15 and 16). Benomyl was detected in higher concentrations than all other fungicides in both leaves and stems whether it had been applied at 1,500 or 500 $\mu\text{g}/\text{ml}$. Bravo-6F could

Table 15.—Effect of soil drenches on uptake and translocation of fungitoxic materials by sugar maple seedlings.

Fungicide and Concentration ^a	Tissues and Portions of Plant Sampled ^b					
	Leaves			Wood ^c		
	Terminal	Center	Lower	Top	Center	Bottom
Diameter of zone of inhibition (mm)						
Benomyl						
1,500	27	34	41	21	19	23
500	18	23	24	13	17	17
Thiabendazole						
1,500	18	23	25	14	16	18
500	13	16	17	9	11	11
Bravo-6F						
1,500	0	0	0	0	0	0
500	0	0	0	0	0	0
Vitavax						
1,500	19	25	28	16	21	23
500	16	15	18	14	13	12
Control	0	0	0	0	0	0

^a Fungicides applied three times as a soil drench at the rate of 200 ml of aqueous suspension per pot. Plants bioassayed 30 days after last treatment. Concentration at $\mu\text{g}/\text{ml}$ active ingredient-aqueous suspension.

^b Leaf disc (9 mm diameter); wood sections (10 mm long).

^c Top (characterized by fully expanded terminal leaves); bottom (5 cm above severed base of stem).

Table 16.—Effect of soil drenches on uptake and translocation of fungitoxic materials by Russian olive seedlings.

Fungicide and Concentration ^a	Tissues and Portions of Plant Sampled ^b					
	Leaves			Wood ^c		
	Terminal	Center	Lower	Top	Center	Bottom
Diameter of zone of inhibition (mm)						
Benomyl						
1,500	18	19	22	13	15	15
500	12	13	16	8	11	12
Thiabendazole						
1,500	16	16	18	11	13	14
500	9	9	11	5	6	6
Bravo-6F						
1,500	0	0	0	0	0	0
500	0	0	0	0	0	0
Vitavax						
1,500	10	11	13	6	6	7
500	8	10	10	5	6	6
Control	0	0	0	0	0	0

^a Fungicides applied three times as a soil drench at the rate of 200 ml of aqueous suspension per pot. Plants bioassayed 30 days after last treatment. Concentration at $\mu\text{g}/\text{ml}$ active ingredient-aqueous suspension.

^b Leaf disc (9 mm diameter); wood sections (10 mm long).

^c Top (characterized by fully expanded terminal leaves); bottom (50 mm above severed base of stem).

not be detected in any plant tissue above ground. A higher concentration of the fungitoxicant accumulated in the sugar maple seedlings than in the Russian olive seedlings. The bioassay of foliage and wood from the sugar maple produced zones of inhibition approximately twice as large as those from Russian olive seedlings.

FOLIAR TREATMENTS.—A foliar application of benomyl, dissolved in lactic acid or sulfuric acid, 2 weeks prior to soil infestation gave the best control (Fig. 18). Benomyl suspended in water gave less control than either application of benomyl dissolved in acid. When the application of benomyl was delayed for 2 weeks after soil infestation, little control occurred. All foliar applications, regardless of formulations, gave better control if they were applied prior to soil infestation.

Benomyl, or a benomyl derivative, was detected moving upward to areas of new growth after it had been applied to localized areas at 5,000 $\mu\text{g}/\text{ml}$. After applications had been made to the top three leaves of sugar maple

seedlings, a fungitoxic material could be detected in the treated leaves, but no fungitoxic material was found moving downward in the wood. After a benomyl derivative was applied to the lower two branches and leaves, a fungitoxic material was found in the foliage and vascular wood of the treated area, and also in the untreated foliage and wood above the point of application. When applications were made to leaves on one side of the plant, a fungitoxic material was found adjacent to the treated area and upward in the nontreated areas. Therefore, a benomyl derivative was translocated from the treated areas to adjacent nontreated areas above the point of application. No fungitoxic materials were detected below the point of application.

ROOT TREATMENTS.—Root infection of sugar maple and Russian olive seedlings can be reduced and symptom expression delayed by dipping the roots with fungicides before placing them in infested soil (Table 17). Benomyl, TBZ, Bravo-6F, and Vitavax all gave some degree of control against Verticil-

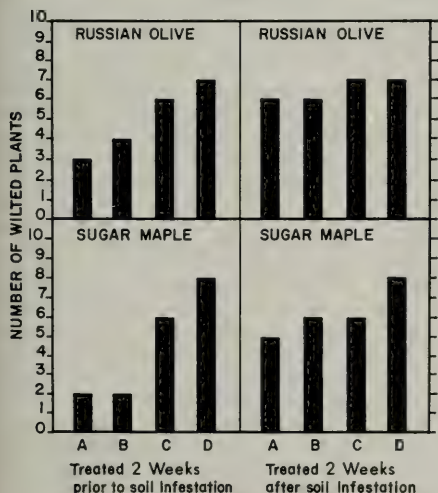


Fig. 18.—Degree of Verticillium wilt control with various foliar applications of benomyl: A) Benomyl/lactic acid/water; B) Benomyl/sulfuric acid/water; C) Benomyl/water; D) Control.

Table 17.—Effect of root treatments on symptom expression of sugar maple and Russian olive seedlings planted in *Verticillium albo-atrum*-infested soil.

Fungicide ^a	Plants Treated	Days After Treatment	Percentage of Plants Wilted
		for Initial Symptom Expression	
<i>Sugar maple</i>			
Benomyl	10	28	40
Thiabendazole	10	21	60
Bravo-6F	10	14	70
Vitavax	10	18	50
Control	10	7	80
<i>Russian olive</i>			
Benomyl	10	17	30
Thiabendazole	10	14	50
Bravo-6F	10	12	60
Vitavax	10	13	50
Control	10	8	70

^a Fungicides applied as a root dip for 5 minutes at the rate of 1,500 µg/ml.

lium wilt. On sugar maple and Russian olive seedlings, benomyl was much more prophylactic in protecting against root infection than the other fungicides tested. All fungicides used as a prophylactic delayed initial symptom development. Symptoms on sugar maple seedlings treated with benomyl developed 21 days later than symptoms on the control. Initial wilt symptoms on benomyl-treated Russian olive seedlings occurred 9 days later than those on the control.

DISCUSSION AND CONCLUSIONS

The control of a vascular wilt pathogen is extremely difficult. Systemic fungicides which can be applied to the soil, taken up by the root system, and translocated throughout the plant are the most feasible. Fungicides applied prior to infection may serve as a barrier which will kill or arrest the fungus before it becomes established. The application of a systemic fungicide, which will inhibit growth of the fungus after symptoms appear, may be a more logical control measure.

The in vitro assay for fungicide toxicity appears to be quantitative using the agar diffusion method. There is a proportional increase in size of the zone of inhibition with increase in

quantity of the fungicide. The difference in inhibition may not be related as much to differences in toxicity of the chemical as to solubility and diffusibility. The in vitro data indicate that these fungicides are fungitoxic at low concentrations and that benomyl or its toxic breakdown product exists in plant tissue at a point beyond the place of application.

Benomyl, TBZ, and Vitavax, when applied as soil drenches, reduced symptom development after plants had become infected. The inability of any fungicide to give 100 percent control may be due to the tyloses and gum-like materials which inhibit the fungitoxicant from being translocated to the foliage. Recovery of the fungitoxicant from wilting plants that showed vascular plugging was limited. If the fungicide was applied before vascular plugging took place, the fungitoxicant readily moved throughout the plant and could be assayed in the above-ground parts. Fungicides, such as Bravo-6F, which show no systemic action are of little value in controlling *Verticillium* wilt when applied as a soil drench.

Benomyl dissolved in either an organic or inorganic acid and applied to the foliage gave better control than a benomyl suspension in water. With

the addition of acids, the fungitoxicant was water soluble, and could be taken up more readily and translocated throughout the plant. The fungitoxicant must be localized in the plant parts before the host-pathogen interaction produces gums and tyloses, blocking the upward movement of the fungitoxicant. Once wilt symptoms occurred and the vascular system was occluded, translocation of the fungitoxicant was reduced regardless of the formulation.

The time of fungicide application is critical for the fungitoxicant to be distributed throughout the plant before the fungus can become established. The critical time of application was similar for foliar treatments and soil drenches.

When fungicides were tested as prophylactic root dips, each gave some degree of control. Initial wilt symptoms were delayed as much as 3 weeks with benomyl. The delaying of root infection may allow wounds to be occluded with wound material before the fungus can become established at the wound site. This method of control may be of value when used on bare-rooted nursery materials.

More work is needed to determine how fast these systemic fungicides will move in the plant and how long they will remain active. Additional work is needed to determine the critical time of application and if higher concentrations will be more effective but not phytotoxic to the host.

SUMMARY

Verticillium albo-atrum Reinke and Berthold is a widespread and destructive vascular pathogen. It is peculiar in that it does not confine its attack to one host, or a few closely related hosts, but attacks a large number of widely unrelated plants, many of which are of economic importance.

The wound most conducive to infection was a vascular wound which

allowed the pathogen to come in direct contact with the vessel members. No infection took place unless a wound was present on the root. Root wounds remained as infection courts up to 32 days on redbud and 16 days on sugar maple seedlings. As the age of the wound increased, the number of plants infected through wounds decreased sharply.

In the susceptible hosts, the pathogen rapidly colonized the cortex, endodermis, and vessel members. Conidia were produced in abundance within 8 days. The pathogen in the resistant hosts readily colonized the cortex, but few hyphae were found in the vessel members. Conidia were not present in the vascular system. Microsclerotia were found in both the cortex and vascular cylinder of the resistant hosts.

Infection leads to a significant reduction in dry-matter production, stem height, and leaf area of the plants. The nitrogen content was lower in infected redbud and green ash stems, but higher in leaves and roots. There was no definite pattern of water content between infected and healthy redbud and green ash seedlings. Frequently the water content of the infected seedlings was above that of the healthy controls, but not consistently.

Abundant microsclerotia were observed in roots after 14 days when incubated at 15, 20, 25, and 30 C. Microsclerotia were observed after 35 days at 5 and 10 C, but no microsclerotia were observed at 35 C. Microsclerotia developed in dead roots incubated at 25 C in both steamed and nonsteamed soil. A moisture level near the field capacity of the soil was more favorable for microsclerotial development than was a lower soil moisture.

The *in vitro* assay of the toxicity of the fungicides by the agar diffusion method appears to be quantitative. There is a proportional increase in the size of the zone of inhibition with increase in quantity of the fungicide.

Benomyl, TBZ, and Vitavax, when applied as soil drenches, reduced symptom development after plants had become infected. The inability of any fungicide to give 100-percent control may be due to the host-pathogen interaction producing tyloses and gum-like material which prevents the fungitoxicant from being translocated to the foliage. Fungicides which show no systemic action are of little value in controlling *Verticillium* wilt when they are applied as a soil drench.

Benomyl which had been solubilized in either an organic or inorganic acid

and applied to the foliage gave better control than a benomyl suspension in water. With the addition of acids, the fungitoxicant was water soluble, and could be taken up more readily and translocated throughout the plant.

When the fungicides were tested as prophylactic root dips, all delayed symptom expression and gave some degree of control. Benomyl delayed initial wilt symptoms as much as 3 weeks. The delaying of root infection may allow wounds to be occluded with wound material before the fungus can become established at the wound site.

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Frontispiece.—A hangingfly, **Bittacus pilicornis**, awaiting its prey, which includes mosquitoes and other bottomland insects. (Photo by W. D. Zehr)

The Mecoptera, or Scorpionflies, of Illinois

Donald W. Webb, Norman D. Penny, and John C. Marlin

THE ORDER MECOPTERA (scorpionflies and hangingflies) is of ancient lineage. Fossils of this order are known from as far back as the Permian. Today relatively few species of Mecoptera exist; fewer than 500 are currently recorded for the world. They and their fossil relatives exhibit many primitive characteristics and are considered among the oldest and most primitive holometabolous insects. Eighteen species occur in Illinois. They live in mesic places, especially among dense herbaceous vegetation in lowland woods. One species of *Boreus* occurs only on moss in woods and is a relict of the Arctotertiary forest. This species is found in the southwestern corner of the state.

Twenty-one families of Mecoptera are recognized, a dozen of which are represented only by fossils. Of the nine extant families, the Bittacidae (hangingflies) are the most widespread, occurring on all continents in tropical and warm-temperate regions. The families Notiothaumidae (found only in South America) and Meropeidae (one monotypic genus in Australia and one in North America) are considered the most primitive. Three families, Choristidae, Nannochoristidae, and Apteropanorpidae, are restricted to the southern hemisphere, occurring in Australia, Tasmania, or New Zealand. The remaining three families, Boreidae, Panorpididae, and Panorpidae, are found in North America and Eurasia.

The five families (Bittacidae, Boreidae, Meropeidae, Panorpididae, and Panorpidae) occurring in North America contain 80 species. The majority of these species are distributed throughout the eastern United States. Other species occur in Central America, Mexico, and the western coastal states. With the exception of the family

Boreidae, no Mecoptera have been recorded north of the 50th parallel in North America.

The center of distribution of Mecoptera in the United States is in the southern Appalachians (Byers 1969), from which area the various species have dispersed themselves northward and westward. Thirty-two species are recorded in the Midwest. Illinois, with its extensive north-to-south length and geological history, provides a wide variety of habitats for most groups of Mecoptera. The glaciated regions of northern Illinois, in particular the Northeast Morainal Division¹, offer suitable habitat for species, such as *Panorpa subfurcata*, *P. mirabilis*, and *P. galerita*, distributed primarily or wholly in previously glaciated areas. The Coastal Plain Division (Austroriparian Division) at the southern tip of Illinois is attractive to those species, such as *Panorpa nuptialis*, distributed in the coastal plains of the southern Atlantic and Gulf states. The narrow strip of Ozark Division in southwestern Illinois is an extension of the Ozark uplift and provides habitats for species such as *Panorpa braueri*. Similarly, the Shawnee Hills Division of southern Illinois contains habitats similar to those in the southern Appalachians and in Kentucky and Tennessee for such species as *Bitacrus punctiger*. The central part of Illinois has areas of deciduous forest along the eastern boundary and prairie and mixed woodland to the west that provide habitats for the other midwestern species.

The objective of this study is to update our knowledge of the distribution and natural history of Mecoptera, particularly in relation to the biogeographic

¹ Terms from "The Natural Divisions of Illinois," Illinois Nature Preserves Commission, 1972.

history of Illinois. Synoptic descriptions, keys, and illustrations have been prepared to provide an insight into this primitive and interesting group of insects.

The emphasis of this study is on the fauna of Illinois, but other species occurring in the Midwest have been included.

Collecting data are listed for those Illinois species known from fewer than ten localities. Records for other species are plotted on distribution maps.

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NATURAL HISTORY

Feeding

In the Bittacidae, adults of *Bittacus* and *Apterobittacus* are predaceous. Hanging by their fore or, occasionally, middle legs from the underside of vegetation, they wait with outstretched hind legs for some unsuspecting prey. When prey is within reach, it is seized by the raptorial tarsi of the hind legs. The prey is brought to the mouth, and the piercing mouthparts enter through the intersegmental membranes. The soft body parts of the victim are withdrawn, and the empty exoskeleton is discarded. *Bittacus* feed on a wide variety of insects. In Illinois *Bittacus apicalis*, *B. strigosus*, and *B. pilicornis* feed heavily on dolichopodids (Diptera). Setty (1931 and 1940) and Newkirk (1957) listed a wide range of insects that *Bittacus* accept, noting a preference for Diptera and Homoptera.

The time required for feeding varies considerably. Setty (1931) reported the average time as 20 minutes although feeding sometimes lasted as long as 40 or 50 minutes. Newkirk (1957) reported that the feeding of *Bittacus apicalis* may last an hour. He gave a detailed account of *B. apicalis* feeding on aphids:

The hangingfly regurgitates a dark-brown fluid, which resembles the "tobacco juice" of a grasshopper, and covers a part of the aphid with it. Through this the hangingfly bites, and sucks out the aphid body fluid. Then the hangingfly injects saliva, kneads what is left in the aphid body cavity with its mandibles, draws off the mixture; re-

peats this several times; and discards the empty exoskeleton.

Very young larvae of bittacids are relatively active, but older larvae move very little (Setty 1940) and can be found among ferns and moist leaf litter in humid lowland woods. They feed on dead or dying animal matter, and it is not known if they can catch live prey.

Little is known of the feeding habits of *Boreus*. Withycombe (1922) observed the larvae and Fraser (1943) the adults of *Boreus hyemalis* feeding on moss. Other substances may also be consumed. In Illinois, *Boreus* lives in *Atrichum angustatum* and probably feeds on it.

Nothing is known of the feeding habits of the family Meropeidae.

The feeding habits of the Panorpidae, in particular *Panorpa*, have been variously reported in the literature. Lyonnet (1742) initiated the misconception that *Panorpa* are predaceous when he saw a fly the size of a scorpionfly attack a damselfly and bring it to the ground. Kirby & Spence (1823) repeated Lyonnet's description and asserted that the species involved was *Panorpa communis*. Since then, numerous authors (Brauer 1863; Byers 1963; Campion & Campion 1912; Felt 1895; Lucas 1910; Miyaké 1912; Shiperovitch 1925; and Syms 1934) have published observations on panorpids' feeding, and none has been found to be predaceous. Panorpids feed primarily on dead or dying insects although Carpenter (1931b) reported their feeding on the nectar of flowers, and Miyaké (1912) saw them feeding on the petals of sweet william.

Larvae of *Panorpa* feed principally on dead or dying animal matter, but Felt (1895) reported larger larvae of *Panorpa* attacking and devouring smaller ones.

Mating and Oviposition

Setty (1940) and Newkirk (1957) gave detailed descriptions of the mating of *Bittacus*. The description here is a compilation of both. The male seizes

a prey and flies from leaf to leaf in search of a female. When at rest, he vibrates his hind wings, opens and closes his claspers, and bends his abdomen vertically, everting and inverting his abdominal sacs. Both male and female hang by their fore legs facing each other, and the male offers the prey to the female, which she eats during mating. In some instances the female jabs with her mouth at the male abdominal tip, where the eversible sacs are located, or at the prey. The male secures her abdomen in his claspers, then moves along the ventral surface to the terminalia. Only the female feeds during copulation. The length of copulation is proportional to the palatability of the prey and lasts from 1 to 25 minutes. When copulation is completed, the abdominal tips separate, and the individuals jerk at each other to disengage the legs. Both male and female may mate more than once.

During oviposition the female rests on the ground with her head bent down and legs sprawled outwards. The body is quite rigid and the tip of the abdomen is inserted into cracks in the soil. Oviposition takes from 5 to 30 minutes, and several eggs are laid at a time. The female may fly from place to place and lay a few eggs in each. Oviposition occurs during the day or night. In captivity females tend to lay eggs randomly on the soil surface rather than in some place of concealment.

In the Boreidae the mating behavior of the European species *Boreus hyemalis* has been reported by several authors (Brauer 1855; Lestage 1920; Steiner 1937; Stitz 1908; Syms 1934; and Withycombe 1922). Cockle (1908) described the mating of *B. californicus*. Carpenter (1936), Crampton (1940), and Cooper (1940) described the mating of *B. brumalis*. The description given here is based on the observations of Cooper (1940) on *B. brumalis*.

The male approaches to within 10 mm or so of the female, and both remain momentarily stationary. The male may show his excitement by slowly

waving his antennae or twitching his claspers and wings. He springs at the female with his claspers in advance, seizing the antenna, tibia, or tarsi of the female. The female becomes immediately passive, and the male seizes her about the body with his modified wings. Once the female is securely gripped with his wings, the male employs his hind legs and claspers to right the female and move her venter across his back until his terminalia clasp her apical abdominal segments. The eighth sternum of the female is pried down by the male's claspers, which are inserted into a pair of pockets on the male's ninth tergum. The male releases his wings from the female, and she then flexes her rostrum between her coxae, folds her antennae between her legs, and stretches her legs posteroventrally. Once the female is in this position, the male grips her profemora and rostrum with his clasping wings. This position is maintained throughout copulation of 1-12 hours. The male may run about and feed during copulation, while the female remains motionless. This pattern of behavior follows closely observations made on *B. californicus* and *B. hyemalis*.

According to Carpenter (1931b), *Boreus* lays eggs one or two at a time at the bases of moss clumps. Nothing has been reported on the mating behavior or oviposition of the Meropeidae.

In *Panorpa* mating is relatively simple (Miyaké 1912). The male vibrates his wings as he approaches the female. The apex of the abdomen is extended with the claspers securing the abdomen of the female. The claspers are moved along the abdomen until the terminalia are reached and the individuals are at an acute angle to each other. In addition, Mickoleit (1971b) noted the use by *P. communis* of the notal and post-notal organs as pincerlike devices for holding the costa of the female during copulation. Copulation lasts for 15 minutes to several hours. Although the mating behavior of *Panorpa* is simple,

there is one peculiarity that has led to some controversy. Mercier (1915) noted that prior to copulation in *P. germanica*, *P. alpina*, and *P. cognata* the male was seen to emit from its mouth a drop of fluid that hardened into an opaline pellet, which it placed on the soil. The female then fed on the pellet during copulation. When the pellet was consumed, another was produced. Shiperovitch (1925) observed males of *P. communis* emitting cylindrical pellets from their mouths, and Gassner (1963) noted that unfed specimens of *P. nuptialis* regurgitated a brownish secretion on which the female fed during coitus. Syms (1934) observed no pellets being released but noted that the female fed on a dead insect during mating. Carpenter (1931b) observed the mating of several species of *Panorpa* but never saw such feeding behavior. One of us (Penny) has observed the depositing of salivary pillars by *P. speciosa*, *P. nuptialis*, *P. anomala*, and *P. helena*. Byers (1963) observed no salivary secretion being produced by the male of *P. nuptialis* although Gassner (1963) did observe this phenomenon. In observing the mating of *P. sigmoides*, Webb saw no evidence of a salivary secretion or pellet being offered by the male, nor did the female feed during copulation. In the field *P. sigmoides* was also observed to mate during the hours of daylight. Most authors have observed mating during the hours of darkness, but Byers (1963) found *P. nuptialis* to mate only during the daylight hours.

During oviposition the female probes the surface of the soil for an appropriate crevice, and the abdomen is extended and inserted deeply into the soil. The number of eggs laid at one time varies.

Immature Stages

In *Bittacus* the size and shape of the eggs vary considerably among the species. The eggs range in length from 0.56 to 0.72 mm and in width from 0.41 to 0.65 mm (Setty 1940).

In *B. apicalis* the eggs are oval (Fig. 1) or spherical and have a finely reticulated surface. In *B. punctiger*, *B. strigosus*, *B. occidentis*, *B. stigmaterus*, and *B. pilicornis*, the egg shape varies from cuboidal to heptahedral, and the egg has a shallow depression on each side (Fig. 2). The surface is rough and has numerous small protuberances.

Prior to hatching, the eggs become spherical and increase in size (Setty 1940). *B. punctiger* and *B. pilicornis* eggs hatch within 2 weeks, and the immatures overwinter as larvae. *B. strigosus*, *B. apicalis*, and *B. stigmaterus* pass the winter in the egg stage.

The newly hatched larva emerges through an irregular crack in the wall of the egg and feeds on the remnants of the egg shell. The larvae do not burrow through the soil in search of food, but the older larvae lie motionless on the surface among the leaf litter and ground debris. The larvae pass through five instars before pupating (Setty 1940).

The larvae of *Bittacus* (Fig. 3) are cylindrical and range in length from 11 to 14 mm in the last instar. The heavily sclerotized head is broad anteriorly. In lateral view the head is oval or elliptical. It is generally bent under the body so as to be completely hidden from above by the thorax. The antennae are short and stout and have only two segments. The single median ocellus is present as well as two large lateral eyes, which are not true compound eyes, according to Setty (1931 and 1940), but simply a group of several ocelli. The mandibles are large and heavily sclerotized and bear several

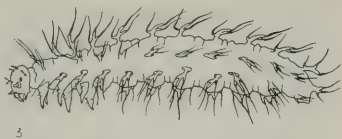


Fig. 3.—*Bittacus strigosus* larva.

large teeth. The labial and maxillary palps are short and stout and have two and four segments, respectively. The head bears numerous coarse setae and tubercles. Each of the three thoracic segments bears a pair of sharply pointed legs, and each of the first nine abdominal segments possesses a pair of short ventral prolegs. The last abdominal segment bears a ventral protrusible sucker that aids in locomotion. The dorsal and lateral margins of the thorax and abdomen bear several simple or branched protuberances, each with a simple or clavate apical seta. Individuals collected in the field usually are covered with soil which clings to these setae and protuberances.

The larvae are negatively phototropic and prefer moist shaded areas. Prior to pupation the fourth instar larva burrows into the soil, forming a diagonal cylindrical chamber (Setty 1940). The larva constructs a collar around the opening with a thin layer of soil laid across it. At this time the larva molts to form a prepupa. The prepupa remains in the bottom of the chamber, for 9–18 days in the case of *B. punctiger* (Setty 1940), following which it metamorphoses into a pupa.

In the case of *B. punctiger*, the pupa remains in the chamber for 13–20 days (Setty 1940), after which the adult emerges through the opening that the larva had entered.

Setty (1931, 1939, 1940, and 1941) has done extensive work on the morphology and behavior of the North American species of *Bittacus*, and much of the description of the immature stages presented here was extracted from his publications.

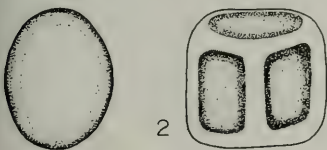


Fig. 1–2.—*Bittacus* eggs. 1.—*B. apicalis*. 2.—*B. strigosus*.

In North America the complete life history of *Boreus* has not been published for any species. The description presented here is for *B. hyemalis*, as described by Withycombe (1922 and 1926).

The eggs of *Boreus* are about 0.5 mm long and 0.3 mm wide. They are laid at the base of moss, and the larvae hatch in about 10 days, usually in late fall. The larvae pass through four instars, a mature larva (Fig. 4) being 6–7 mm long. The head is pale yellow and heavily sclerotized. The eyes are small and composed of several small facets. Mandibles are large, dark brown, and heavily sclerotized. Antennae are small and have two segments and a fine apical bristle. Labial palps are small. The thorax is pale white and broad and has three pairs of ventrolaterally extended legs. The legs have three segments, the basal segment being broad and the others tapering to a small, acute apical segment. The abdomen is pale white and without lateral appendages and has the apex rounded. Each segment has several fine setae.

The larvae appear to aestivate throughout the summer in small cells made in compacted soil in which they pupate in late fall. The duration of the pupal stage is 4–8 weeks.

Nothing is known of the immature stages of the Meropeidae.

In *Panorpa* the size and characteristics of the egg vary considerably. In the *lugubris* group the eggs of *P. nuptialis* are spherical or oval with a smooth surface and measure about 1.07

mm in length and 0.84 mm in width when laid (Byers 1963). In the *rufescens* group the eggs of *P. helena* are oval, have a fine network of depressions covering the surface, and measure about 1.10 mm in length and 0.65 mm in width. Felt (1895) described the eggs of *P. debilis* (as *P. rufescens*) as elliptical and oval, 0.625 mm long, and 0.6 mm wide. Numerous authors (Brauer 1852; Byers 1963; Felt 1895; Syms 1934; and Yie 1951) have observed that the color of the egg darkens before hatching. The duration of the egg period is about 8 days for *P. nuptialis* (Byers 1963) and 6–7 days for *P. debilis* (Felt 1895).

Gassner (1963) observed an egg burster on the frons of the first instar of *P. nuptialis*. It is used in rupturing the chorion of the egg. According to Gassner, the larva assumes a flattened spiral position prior to hatching. It expands and forces the egg burster through the chorion. The larva then makes a quarter turn and slices open the shell.

The larva of *Panorpa* (Fig. 5) is elongate and cylindrical. It passes through four larval instars before pupation (Boese 1973; Byers 1963; Mampe & Neunzig 1965; Shiperovitsh 1925; Yie 1951). Based on measurements of head width, Felt (1895) reported *P. debilis* (as *P. rufescens*) as having seven larval instars, as Miyaké (1912) reported for *P. klugi*. Carpenter (1931a) also described *Panorpa* as having seven instars. The antennae are short and stout and have a scape, a pedicel, and one flagellar segment. The eyes are composed of 25 or more facets. The mandibles are large and heavily sclerotized and have two to four mesal teeth.

The thorax bears a pair of short

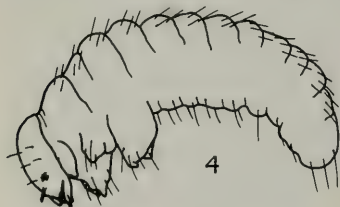


Fig. 4.—*Boreus brumalis* larva.

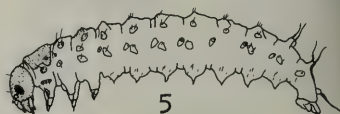


Fig. 5.—*Panorpa* sp. larva.

pointed legs on each segment and a thick sclerotized pronotal shield. A single pair of spiracles is present on the pronotal segment. The thorax and the abdomen bear numerous setigerous prominences (pinacula) and unmodified setae. The eighth and ninth abdominal segments each possess a pair of annulated setae borne on moderately sclerotized projections and a single annulated seta on segment 10. A pair of prolegs and a lateral spiracle are present on abdominal segments 1-8. Four translucent, retractible anal lobes and a basal fold of skin comprise the 11th segment.

Byers (1963) reported in detail on the life history of *P. nuptialis*, from which much of the information presented here has been taken. Boese (1973), Felt (1895), and Mampe & Neunzig (1965) have described other North American larvae. Several authors have described the immature stages of European and Asian panorpids (Brauer 1863; Miyaké 1912; Shiperovitsh 1925; Steiner 1937; and Yie 1951).

After hatching, the larvae burrow farther into the soil and feed primarily

on decaying organic matter although Felt (1895) reported some larvae as being predaceous.

The larvae spend 4-5 days in each of the first three instars and are active and feed for about 2 weeks in the fourth instar, following which the full-sized larvae become quiescent and construct prepupal cells. The prepupal cell is oblong with rounded ends and is formed in compacted soil. The cell is about as long as the larva but possesses no visible lid, like that noted by Yie (1951) in Formosan panorpids. The larvae then enter a prepupal or quiescent stage, which carries them through the winter.

The duration of the pupal stage varies from 6 to 21 days. Prior to emergence the pupal skin splits along the dorsal midline, and the adult emerges. The hour of emergence is dependent upon the species. Yie (1951) found that in Formosan panorpids emergence occurred most often in the early morning.

Habitat

In the Bittacidae most species are restricted to the humid, well-shaded

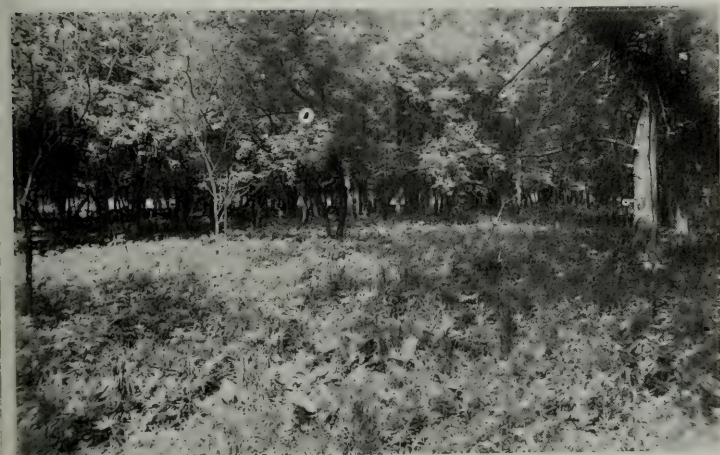


Fig. 6.—Herbaceous vegetation in lowlands along the Illinois River, Starved Rock State Park, Illinois. (Photo by H. H. Ross, courtesy of Section of Botany and Plant Pathology, Illinois Natural History Survey)



Fig. 7.—Deciduous forest and herbaceous vegetation along creek bed at Trestle Hollow, Fountain Bluff, Jackson County, Illinois. (Photo by W. D. Zehr, courtesy of Section of Botany and Plant Pathology, Illinois Natural History Survey)



Fig. 8.—*Bittacus apicalis* hanging from herbaceous vegetation. (Photo by W. D. Zehr)

areas along streams and in bottomlands (Fig. 6 and 7). Individuals (Fig. 8 and 9) can be found hanging from the undersides of leaves of jewelweed (*Im-*



Fig. 9.—*Bittacus pilicornis* hanging from herbaceous vegetation. (Photo by W. D. Zehr)

patiens sp.), stinging wood nettle (*Laportea canadensis*), gooseberry (*Ribes* sp.), and a variety of other bottomland plants. *Bittacus strigosus* has the widest range of habitats, extending from the moist bottomland areas to the drier hillside areas and occurring predominantly on multiflora rose (*Rosa multiflora*). In western Illinois *B. strigosus* was collected abundantly in short pasture grass in the shade of poplars (*Populus* sp.). Little is known of the habitat for *B. occidentis*. Most of the individuals collected have been taken at lights.

In the Boreidae the various species are highly restricted in habitat. Specimens are collected only in, or very close to, patches of moss on the ground (Fig. 10). In southern Illinois *B. brumalis* lives in *Atrichum angustatum* and *Dicranella heteromalla*.

Of the habitat of the Meropeidae little is known. The majority of specimens have been collected in a variety of hardwood forests but mostly at lights or in Malaise traps. Occasionally indi-

viduals have been found under stones or rotting logs.

The habitats of the Panorpidae are similar to those of *Bittacus*. Individuals of *Panorpa* (Fig. 11) are most commonly collected as they rest on the leaves of stinging wood nettle, poison ivy (*Rhus radicans*), waterleaf (*Hydrophyllum appendiculatum*), jewelweed, and a variety of other broad-leaved plants. Only members of the *lugubris* group shun the shaded humid areas along streams and are found in the short grasses along roadside ditches or in cotton, tobacco, and soybean fields.

DISTRIBUTION AND DISPERSAL

The order Mecoptera is one of the most generalized groups of holometabolous insects and has an abundant fossil record dating back to the early Permian (Tillyard 1935).

The Bittacidae are the most highly specialized family of the Mecoptera.



Fig. 10.—Patches of moss on a hillside in Lake Murphysboro State Park. (Photo by L. J. Stannard)



Fig. 11.—*Panorpa* sp. on herbaceous vegetation. (Photo by W. D. Zehr)

Their tipulidlike appearance, single raptorial claw on the tarsus, and predaceous habit are three of the most significant specializations. Although bittacids have the bulbous basistyles of most of the Mecoptera, the presence of a four-branched sector vein and the absence of a notal organ suggest that this family's specialization began at an early date. Jurassic fossils of *Probit-*

tacus and *Protobittacus* (Tillyard 1935) also suggest early specialization.

In the Nearctic Region the Bittacidae are represented by two genera, *Bittacus* and a wingless form, *Apterobittacus*. *Apterobittacus* is monotypic and found only in central California (Fig. 12) except for one doubtful record from southwestern Colorado. *Bittacus*, the most widespread genus of the Mecop-

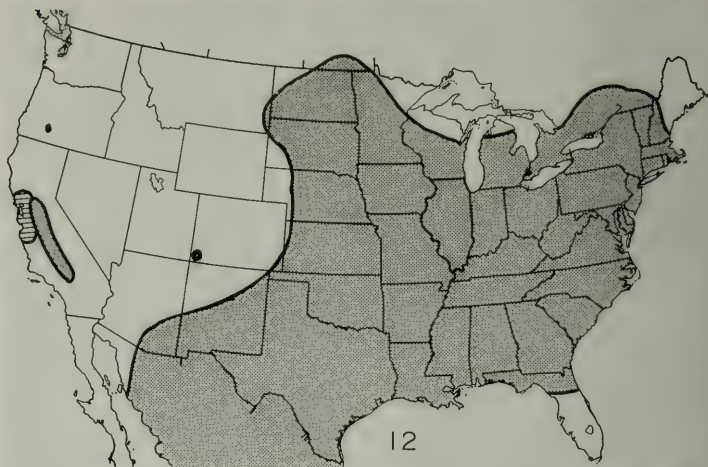


Fig. 12.—General distribution of *Bittacus* (dots) and *Apterobittacus* (lines) in the Nearctic Region.

tera (Fig. 12), extends from northern Florida to Quebec, west to eastern Montana, then south to Mexico, and an isolated species (*B. chlorostigma*) is restricted to California and Oregon.

The spread of the Bittacidae into the Nearctic Region (Byers 1969) possibly occurred during the late Mesozoic or early Tertiary, following the emergence of the Bittacidae prototype on the former southern land mass, Gondwanaland. All bittacid genera, except *Bittacus* and two apparently recent flightless derivatives of *Bittacus*, are restricted to Australia and South and Central America.

After the establishment of land connections between North and South America, *Bittacus* dispersed northward and is known from North American Eocene fossils (Carpenter 1955). Glaciations during the late Pliocene or early Pleistocene then forced the bittacids into the southern United States, Mexico, and South America (Byers 1969). After the glaciations the bittacids in the southeastern United States became sep-

arated from the main bittacid stock in Central America by xeric conditions and the disappearance of mesic forests from northern Mexico and the Southwest. Following the retreat of the glaciers, the southeastern bittacids spread northward and westward, and a second invasion from Mexico brought *B. chlorostigma* to California and *B. texanus* to the Southwest.

Illinois forms the northwest border of the distribution of *B. apicalis* (Fig. 43) and *B. punctiger* (Fig. 44). *B. stigmaterus*, *B. pilicornis*, and *B. strigosus* occur throughout Illinois and extend into the west-central states. *B. occidentis* has been collected only in central and northern Illinois although it is widespread from southern Ontario and New York southwestward to Arizona. Of the midwestern species, only *B. texanus* has not been recorded from Illinois.

The other three North American families (Boreidae, Panorpodidae, and Panorpidae) are all confined to the temperate and boreal forests of the northern hemisphere. All have bulbous

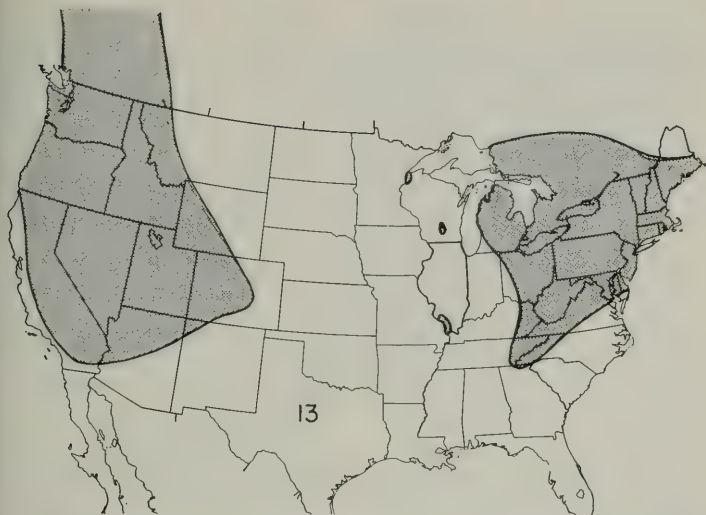


Fig. 13.—General distribution of the Boreidae in the Nearctic Region.

basistyles and pincerlike dististyles. Each has survived in a slightly different climatic zone.

The Boreidae are found primarily in the colder regions of the northern hemisphere from St. Paul Island in the Bering Sea to 12,000 feet in the Colorado Rockies (Fig. 13). In eastern North America the family has spread northward from the southern Appalachians, leaving relict populations in marginal habitats in the southern portions of its range. Adaptations to cold environments include reduction in size, loss of flight and reduction in wing size, and loss of the notal (wing-clasping) organ.

The family Meropeidae is the most primitive family of the Mecoptera in North America. The broad wings with numerous costal crossveins, the short rostrum, and the elongate male basistyles and dististyles indicate the primitive nature of this family. The recent distribution of *Merope* (Fig. 14) (Byers 1973b) indicates the center of specia-

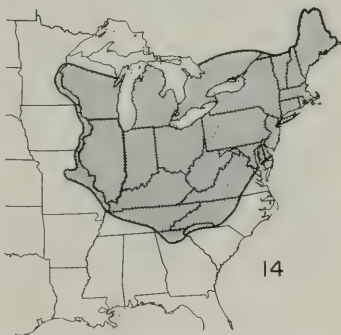


Fig. 14.—General distribution of the Meropeidae in the Nearctic Region.

tion to be in the southern Appalachians, from which area this genus has dispersed northward and to the east and west. Although widespread in the northeastern United States, records of this genus are sparse. In Illinois *Merope* has been recorded only from Pine Hills Ecological Area and Urbana.

The family Panorpodidae is found in boreal environments of montane areas of the southern Appalachian and the northwestern states (Fig. 15). Normally this family is distributed in cool areas from sea level to higher elevations in North America. Adaptations to such boreal environments include the flightlessness of females and the loss of the male notal organ.

The Panorpidae normally live at lower elevations than do the Boreidae and Panorpodidae, but ranges may broadly overlap. Species of the Panorpidae and Panorpodidae from Japan have almost identical wing venation; the North American Panorpodidae (*Brachypanorpa*) have a reduced number of sector branches. The male genitalia of the Panorpidae and Panorpodidae are also very similar, indicating a close relationship between these two families. However, Oligocene Baltic amber has yielded specimens of both *Panorpa* and *Panorpodes* so different that these families must have diverged before the Oligocene.

The majority of Nearctic Panorpidae are distributed in the eastern United States, and several species are recorded from the Southwest and Mexico (Fig. 16). Byers (1969) partitions the genus *Panorpa* north of Mexico into six distributional groups:

1. Those species occurring only in the southern Appalachians. This group contains five species found only at the middle to higher elevations.
2. Those found in the southern Appalachians but also distributed widely to the northeast, northwest, and west. This group contains eight widely distributed species. All extend into the Midwest, and four species occur in Illinois (*P. banksi*, *P. debilis*, *P. helena*, and *P. nebulosa*).
3. Those occurring primarily in the Piedmont and sometimes up into the valleys of the Appalachians. Species in this group occur principally on the eastern side of the Appalachians although both *P. consuetudinis* (= *P. elaborata*) and *P. rufescens* extend into the Midwest.



Fig. 15.—General distribution of the Panorpodidae in the Nearctic Region.

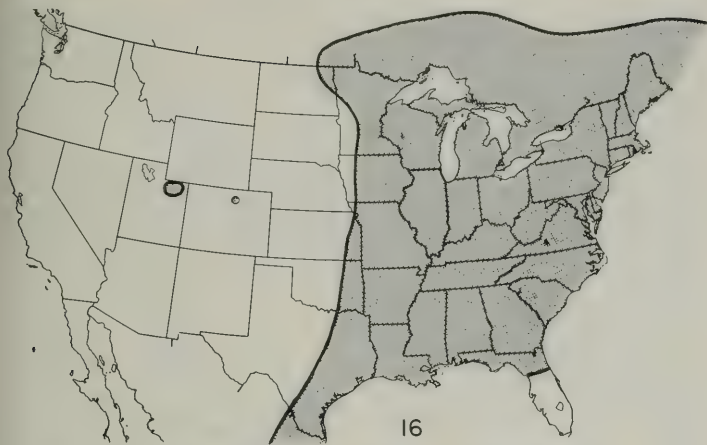


Fig. 16.—General distribution of the Panorpidae in the Nearctic Region.

4. Those inhabiting the coastal plain from Texas eastward to Florida and northeastward approximately to New Jersey. This group contains seven species, only one of which (*P. nuptialis*) extends northward into the Midwest and is known from within 1 mile of Illinois near Cairo.

5. Those occurring primarily or wholly in the formerly glaciated area of the northern Appalachians and westward. The five species in this group all occur in the Midwest to the north and east of Illinois.

6. Those found only in the Midwest. This group contains six species, four of which (*P. anomala*, *P. dubitans*, *P. speciosa*, and *P. stigmoides*) occur in Illinois.

Most species of *Panorpa* inhabit mesic temperate forests with humid, dense undergrowths of herbaceous vegetation. During periods of glaciation in North America these species possibly sought areas of relatively stable climatic conditions (Byers 1969), such as those in the southern Appalachian and Ozark-Ouachita uplift. During interglacial

periods the species spread northward. The southern Appalachian area has the greatest concentration of *Panorpa* species in North America. All the species in Byers' groups one through five and some in group six appear to have arisen from a southern Appalachian ancestral stock and migrated northward and westward. In group six Byers lists six species which occur only in the Midwest. Judging from their present distributions, one can infer that three of them (*P. anomala*, *P. speciosa*, and *P. braueri*) may have differentiated in the area of the Ozark-Ouachita uplift.

COLLECTING AND PRESERVING MECOPTERA

With the exception of the Boreidae, the Mecoptera are generally found on, or hanging from, low herbaceous vegetation in shaded moist woodlands. *Bittacus* can be found by walking slowly through shaded weedy areas and brushing the vegetation back and forth with a net. When disturbed, bittacids will fly 10–20 feet ahead of the collector and

then hang from the vegetation again. The experienced collector may net specimens in flight or follow their flight and collect them as they hang from the vegetation. Some bittacids (*B. apicalis* and *B. occidentis*) have been collected at lights.

The collecting of *Boreus* calls for a rather hardy, determined collector, because these insects reach maturity during late fall and winter. They are associated with mosses on the ground, on bases of trees, and elsewhere. They can be collected by lying beside a patch of moss and waiting for the adults to move. They also move about on patches of snow, where they are easily seen and collected. Larvae of *Boreus* have been taken by Berlese funnel extraction from moss.

The collecting of *Merope* has been accomplished more by chance than by skill. Most specimens have been collected at lights or in Malaise traps in heavily wooded areas.

Panorpa can be collected individually from the surface vegetation. The collector must stalk slowly through the vegetation, particularly stinging wood nettle, until an individual is located. When disturbed, the somewhat sedentary members of this genus will fly a short distance or drop to the ground and escape in the leaf litter. *Panorpa* is seldom taken at lights.

Specimens of Mecoptera can be preserved in 70-percent ethyl alcohol or mounted on insect pins.

The taxonomic characters necessary to separate the genera and many of the species can be seen with a stereoscopic microscope. In the females of *Panorpa*, the genital plate is of taxonomic importance. To observe this plate, one must cut off the tip of the abdomen basal to the eighth segment and boil the tip in 10-percent KOH or leave it overnight in cold 10-percent KOH to remove the soft internal tissues. The tip is transferred to 70-percent ethyl alcohol, and the abdominal terga and sterna are separated with a pair of dissecting points,

revealing the genital plate. In identifying males of some species of *Panorpa*, clearing the genital bulb in 10-percent KOH aids in species determination.

MORPHOLOGY

Several excellent papers have been published on the external and internal anatomy of the Mecoptera (Crampton 1921 and 1931; Dohanian 1915; Grassé 1951; Hepburn 1969 and 1970; Micko-

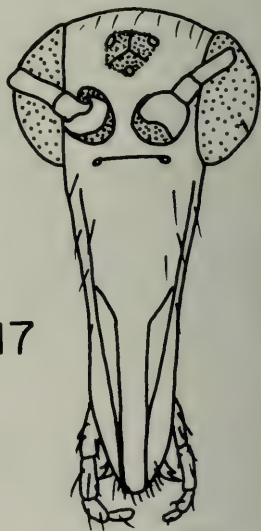


Fig. 17.—*Panorpa helena* anterior view of head.

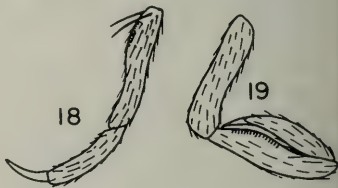
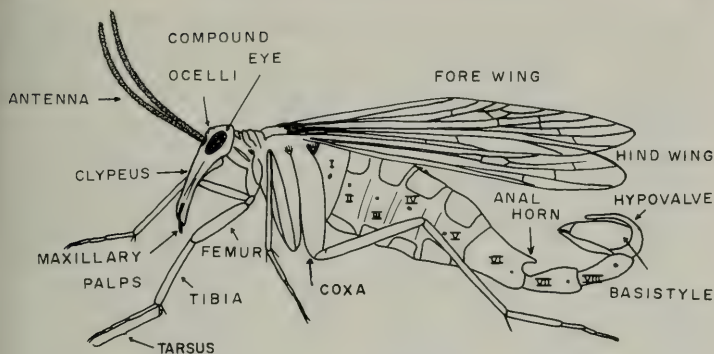


Fig. 18-19.—*Bittacus strigosus*. 18.—Apical tarsal segments with claw. 19.—Apical tarsal segments with claw reflexed.



20

Fig. 20.—*Panorpa* sp. lateral view of male adult.

leit 1971a; Otanes 1922; and Potter 1938).

The descriptions are supplemented with illustrations of the morphological characters of taxonomic importance. Fig. 17 presents an anterior view of the head of *Panorpa*, showing the distinctive elongate rostrum of most of the Mecoptera. Ocelli are present in all genera of the North American Mecoptera except *Merope*. In *Boreus* the

ocelli are indistinct, and numerous authors have reported them absent. In all genera the large, lateral compound eyes are widely separated, except those of *Merope*, which are reniform and almost contiguous dorsally.

The shape and venation of the wings vary from genus to genus. Fig. 24, 50, 64, and 80 illustrate the wings of all midwestern genera. In *Apterobittacus* the wings are absent, and in certain

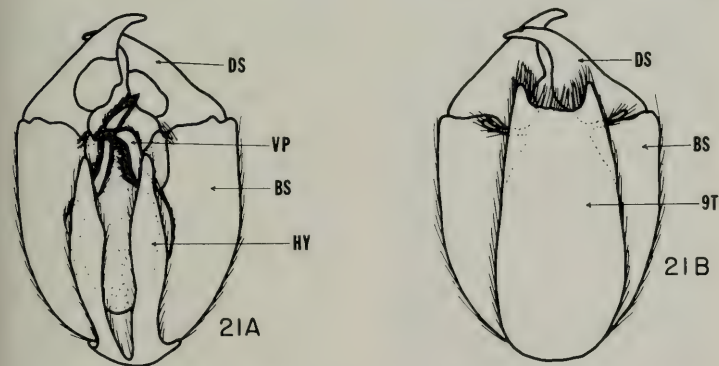


Fig. 21A-B.—*Panorpa sigmoides*. A.—Ventral view of male terminalia. DS, dististyle. VP, ventral paramere. BS, basistyle. HY, hypandrium. B.—Dorsal view of male terminalia. DS, dististyle. BS, basistyle. 9T, ninth tergum.

species of *Brachypanorpa* the females have greatly reduced wings.

The legs in all genera are elongate and cylindrical. In *Panorpa* the apical tarsal segment bears a pair of serrate claws. In *Bittacus* and *Apterobittacus* the tarsi have a single apical claw (Fig. 18 and 19), which reflexes back into a groove in the fourth tarsal segment. This claw is used in holding prey.

Fig. 20 is a lateral view of a *Panorpa* male and illustrates the scorpionlike appearance of the genus. The abdomen is thick and rounded basally and tapers apically to the elongate seventh and eighth segments. The terminalia are bulbous and reflexed over the abdomen. In *Panorpa* the sixth abdominal tergum in males may or may not possess an anal horn.

The terminalia of *Panorpa* are shown in Fig. 21A and 21B, and the morphological characters of taxonomic importance are identified.

MONOGRAPHS ON NEARCTIC MECOPTERA

Because of the small number of species of Nearctic Mecoptera, few major taxonomic revisions have been done on this group. Westwood (1846) in his monograph on the genus *Panorpa* described several Nearctic species. Walker (1853), Hagen (1861), Banks (1907), and Esben-Petersen (1915) catalogued the North American Mecoptera, and Hine (1898 and 1901) reviewed the Mecoptera north of Mexico. In 1908 Sherman reported on the Panorpidae of North Carolina; Engelhardt (1915), the Mecoptera of the northeastern United States; and Esben-Petersen (1921), the North American species. The major revision of the Nearctic Mecoptera was published by Carpenter (1931a) wherein he described many new species. Since then new species have been described and additional distribution data have been reported by Carpenter (1932a, 1935, 1936, and 1939) and Byers (1954, 1958, 1962a, 1962b, and 1973a).

TAXONOMIC TREATMENT

Order MECOPTERA

MECOPTERA Comstock & Comstock 1895

MECAPTERA Packard 1886

PANORPATAE Brauer 1885

The members of the order Mecoptera are moderately large, holometabolous insects, having biting mouthparts generally extended ventrally to form a prolonged rostrum. The antennae are elongate and filiform and have about 20 flagellar segments. The large compound eyes are dichoptic. Ocelli are present or absent. The maxillary palps have five segments.

The thorax is broad dorsally and tapered ventrally. The wings are usually elongate and narrow. The fore and hind wings are nearly equal in length and have numerous veins and crossveins. In several genera the wings are greatly reduced or absent. In *Merope* and *Notiothauma* the wings are very broad and rounded apically. The legs are long and slender and have five tarsal segments, ending in one or two claws. The coxae are large, and each tibia bears a pair of long spurs.

The first abdominal segment is fused to the thorax. The abdomen is generally thick basally and tapered apically except in the Bittacidae. Cerci are present apically in females and subapically in males.

KEY TO THE NEARCTIC FAMILIES OF MECOPTERA

1. Tarsi with single apical claw (Fig. 19) **Bittacidae**
- Tarsi with two apical claws 2
2. Male brachypterous. Female with ovipositor **Boreidae**
- Male with elongate wings. Female without ovipositor 3
3. Wings broad, rounded apically (Fig. 64), with numerous costal crossveins. Ocelli absent **Meropeidae**
- Wings narrow, elongate (Fig. 73), with few costal crossveins. Ocelli present 4
4. Rostrum short **Panorpididae**
- Rostrum long (Fig. 17) **Panorpidae**

BITTACIDAE Enderlein 1910

The raptorial tarsi with a single claw separate the bittacids from other families of the Mecoptera. Twelve genera are distinguished, and their species are recorded from all continents although they are generally absent from the northern parts of Europe, Asia, and North America. *Bittacus* is the most widespread genus, occurring in Europe, Asia, Africa, and North and South America. *Apterobittacus*, found in California, and *Anomalobittacus* from South Africa are the only flightless genera. *Anabittacus*, *Nannobittacus*, *Neobittacus*, *Pazius*, and *Issikiella* occur in South and Central America. *Kalobittacus* is recorded from Central America. *Austrobittacus*, *Edriobittacus*, and *Harporbittacus* occur only in Australia.

Of the two Nearctic genera, only *Bittacus* has been collected in Illinois.

KEY TO THE NEARCTIC GENERA OF BITTACIDAE

1. Wings present *Bittacus*
Wings absent *Apterobittacus*

Apterobittacus MacLachlan

Apterobittacus MacLachlan (1893: 317). Type-species by monotypy. *Apterobittacus apterus* MacLachlan.

Body dark brown, length 20–23 mm, tipuliform. Antennae filiform with 13 flagellar segments. Both sexes wingless. Legs similar to those of *Bittacus*. Abdomen thick, cylindrical. In males, lobes of ninth abdominal tergum in lateral view, broad, subrectangular, extending well beyond apices of basistyles; in dorsal view, narrow, compressed laterally, apices converge. Basistyles broad, thick, fused ventrally. Dististyles small. Aedeagus thick basally, tapering apically to short, looped thread.

This is a monotypic genus probably restricted to California.

Bittacus Latreille

Bittacus Latreille (1805:20). Type-species: *Bittacus italicus* Müller.

Leptobittacus Hine (1898:108). Pro-

posed by Hine for the species *B. strigosus* and *B. pilicornis*. However, Hine retained them in the genus *Bittacus*.

Thyridates Navás (1908:412). Synonymized by Banks (1913).

Diplostigma Navás (1908:413). Synonymized by Banks (1913).

Haplodictyus Navás (1908:413). Synonymized by Banks (1913).

Head small, pale to dark yellow, tapered ventrally to form distinctive rostrum. Eyes large. Ocelli large, amber, on raised subtriangular pad. Antennae long, filiform with 14 flagellar segments.

Thorax broad, compressed laterally. Wings long, narrow, tapered basally. Membranes clear or yellow, often with dark brown apex or crossveins. Subcosta ending in middle of wing. Subcostal crossvein (Fig. 24) usually basal to first fork of radial sector. R_1 forked apically to form pterostigma, which has one or two pterostigmal crossveins. Pterostigma (Fig. 22) darker than surrounding membrane. A whitish thyridium (Fig. 26) around first fork of media. Apical crossvein (Fig. 24) present or absent. Legs elongate, slender, cylindrical. Coxae large, thick, tapered apically. Femora generally slender although hind femora often swollen. Tibiae long, slender with two long spurs. Basal four tarsal segments cylindrical with small apical enlargement; fifth segment fused to apical claw which is reflexed to fit into groove in fourth segment.

Abdomen long, narrow basally. Male terminalia large (Fig. 29). Ninth tergum modified to form two laterally flattened claspers, often extending beyond apices of basistyles. Basistyles broad, fused ventrally, each with short, medially extended dististyle. Aedeagus thick basally, tapering apically. Internal skeleton of female genitalia absent. Sternal region of eighth and ninth segments fused to form subgenital plate. Tenth segment bears pair of unsegmented cerci.

Seven species of *Bittacus* occur in the Midwest.

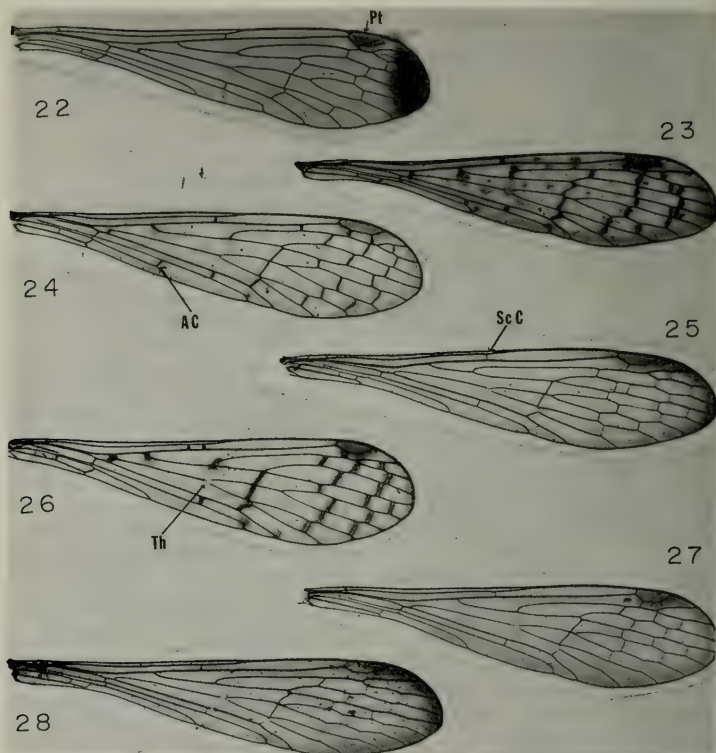


Fig. 22-28.—*Bittacus* fore wings. 22.—*B. apicalis*. Pt, pterostigma. 23.—*B. punctiger*. 24.—*B. pilicornis*. AC, apical crossvein. 25.—*B. occidentis*. ScC, subcostal crossvein. 26.—*B. strigosus*. Th, thyridium. 27.—*B. stigmaterus*. 28.—*B. texanus*.

KEY TO THE MIDWESTERN SPECIES OF BITACUS

1. Apices of wings dark brown (Fig. 22) *apicalis*
Apices of wings not dark brown ... 2
2. Apical crossvein present (Fig. 24) .. 3
Apical crossvein absent (Fig. 25) ... 4
3. Hind femora with brown spot surrounding base of setae *punctiger*
Hind femora without brown spot surrounding base of setae *pilicornis*
4. Subcostal crossvein distal to first fork of radial sector (Fig. 25)
..... *occidentis*
Subcostal crossvein basal to first fork of radial sector (Fig. 26) 5
5. Wing membranes colorless. Cross-

veins margined (Fig. 26) *strigosus*

Wing membranes yellow to pale brown. Crossveins usually not margined (Fig. 27) 6

6. In males, lobe of ninth tergum in dorsal view with two medial prominences, each prominence bearing several black spines (Fig. 40). In females, wing color yellow to amber *stigmaterus*
In males, lobes of ninth tergum in dorsal view with one medial prominence bearing several black spines, and each lobe with a row of 10-15 thick black spines basal to medial prominence (Fig. 42). In females, wing color brown to dark brown *texanus*

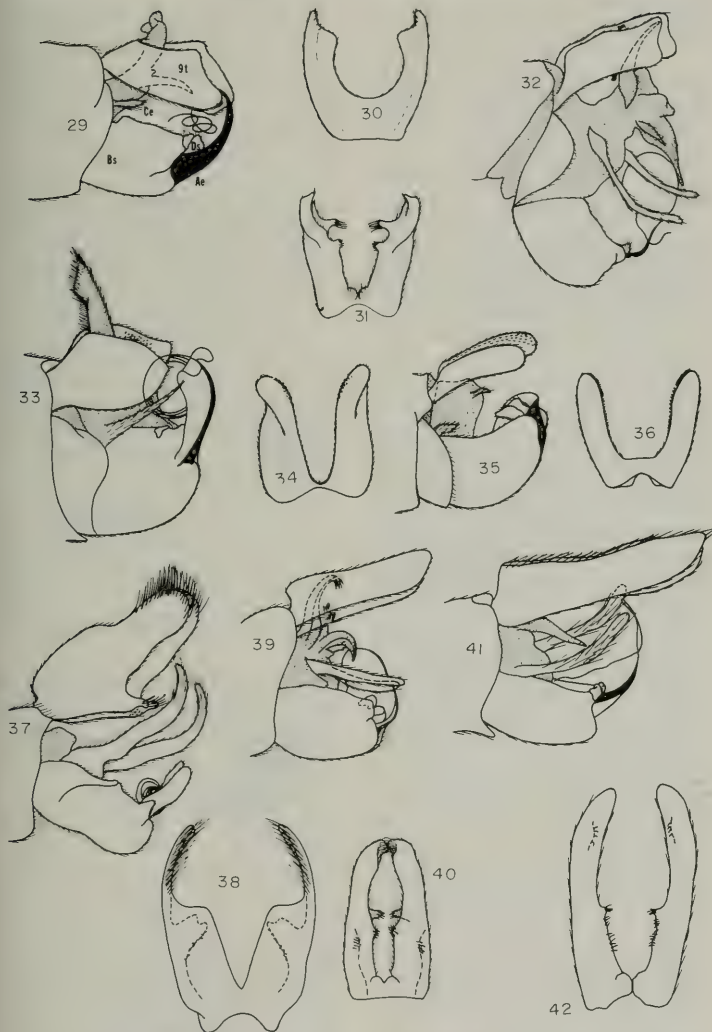


Fig. 29-42.—*Bittacus* male terminalia. 29.—*B. apicalis*. Lateral view of terminalia. 9t, ninth tergum. Ce, cerci. Bs, basistyle. Ds, dististyle. Ae, aedeagus. 30.—Dorsal view of ninth tergum. 31.—*B. punctiger*. Dorsal view of ninth tergum. 32.—Lateral view of terminalia. 33.—*B. pilicornis*. Lateral view of terminalia. 34.—Dorsal view of ninth tergum. 35.—*B. occidentis*. Lateral view of terminalia. 36.—Dorsal view of ninth tergum. 37.—*B. strigosus*. Lateral view of terminalia. 38.—Dorsal view of ninth tergum. 39.—*B. strigosus*. Lateral view of terminalia. 40.—Dorsal view of ninth tergum. 41.—*B. texanus*. Lateral view of terminalia. 42.—Dorsal view of ninth tergum.

Bittacus apicalis Hagen

Bittacus apicalis Hagen (1861:248). ♂, ♀. Type-locality: Southern Illinois.

Haplodictyus incertus Navás (1926:59). ♂. Type-locality: Wilmerding, Pennsylvania. Synonymized by Carpenter (1932*b*).

Head and thorax pale glossy yellow to brown.

Wings (Fig. 22) pale yellow, pterostigma and apex of wing dark brown. Subcostal crossvein basal to first fork of radial sector. One pterostigmal crossvein. Apical crossvein absent.

Legs pale yellow to brown. Hind femora slightly enlarged.

Abdomen and terminalia pale yellow to brown, occasionally eighth tergum of males dark brown to black. In males, lobes of ninth tergum in lateral view (Fig. 29) extend slightly beyond apices of basistyles, dorsal margin with medial prominence; in dorsal view (Fig. 30) lobes diverge apically, curve ventrally, apex with 30 or more black spines. Basistyles broad, thick. Dististyles short, tapered apically. Aedeagus thick at base, tapered apically to slender coiled thread. Cerci short, slender, do not extend beyond middle of basistyles.

The dark brown apices of the wings readily separate this species from all other Nearctic bittacids. When *B. apicalis* hangs from vegetation, the wings are extended laterally from the body (Fig. 8) rather than being folded over the abdomen.

In Illinois *B. apicalis* was collected on jewelweed and stinging wood nettle in moist, shaded, bottomlands along streams. Very seldom were specimens collected on the drier hillsides.

This species extends from North Carolina to New York and west to Illinois, Missouri, and Oklahoma (Fig. 43).

Illinois Records.—(Fig. 43). Collected from early May to mid-August in south and central Illinois. The north-western limit of distribution of *B. apicalis* is in Illinois. No specimens are



Fig. 43.—Distribution of *Bittacus apicalis* in Illinois and North America.

recorded from northern Illinois, Iowa, or Wisconsin.

Bittacus punctiger Westwood

Bittacus punctiger Westwood (1846: 195). ♂, ♀. Type-locality: Georgia. Lectotype ♀ designated by Byers (1962*b*).

Head and thorax pale yellow.

Wings (Fig. 23) dark yellow; heavily patterned with dark brown markings, particularly around crossveins; pterostigma dark brown. Subcostal crossvein basal to first fork of radial sector. Two pterostigmal crossveins. Apical crossvein present.

Legs dark yellow with dark brown band at apices of femora and tibiae. Femora with dark brown spot at base of each seta, particularly on hind legs. Hind femora not noticeably swollen.

Abdomen yellowish brown to dark brown with narrow dark brown strip along posterior margin of each tergum.

Ninth tergum pale yellowish brown, basistyles dark brown. In males, lobes of ninth tergum in lateral view (Fig. 32) rectangular, not extending beyond apices of basistyles, lobe apices emarginate; in dorsal view (Fig. 31) lobes diverge apically, sides straight with two medial prominences, each with several fine black spines. Basistyles broad. Dististyles short, projecting medially. Aedeagus thickened at base, tapering apically to fine looped thread. Cerci elongate, extending slightly beyond apices of basistyles, bases swollen.

This species resembles *B. strigosus* and *B. pilicornis* in the heavily margined crossveins although it is readily separated from these species by the dark brown spot surrounding the base of each femoral seta and the dark brown maculation of the wings.

This species was collected with individuals of *B. strigosus*, *B. apicalis*, and *B. pilicornis* in a moist shaded woodland and among jewelweed.

B. punctiger extends from Florida to Pennsylvania and west to Illinois and Texas (Fig. 44).



Fig. 44.—Distribution of *Bittacus punctiger* in North America.

Illinois Records.—ALEXANDER COUNTY: 1 mile N of Olive Branch, D. W. Webb, 14-VI-1972, 4 ♀; 1 mile E of Olive Branch, Penny and Byers, 30-V-1972, ♂, ♀. FRANKLIN COUNTY: 3 miles S of West Frankfort, 11-VI-1970, J. C. Marlin, 1 ♂. ILLINOIS: Belfrage Collection, Stockholm Museum, 1 ♂,

1 ♀. UNION COUNTY: Pine Hills Ecological Area, 14-VI-1972, D. W. Webb, 4 ♀.

Bittacus pilicornis Westwood

Bittacus pilicornis Westwood (1846: 196). ♂, ♀. Type-locality: America Septentrionali. Type-specimen missing.

Head and thorax dark yellow to dark brown.

Wings (Fig. 24) amber, pterostigma slightly darker than surrounding area, crossveins margined. Subcostal crossvein basal to first fork of radial sector. Two pterostigmal crossveins. Apical crossvein present.

Legs pale yellow to brown. Apices of tibiae and basistarsus dark brown. Hind femora not swollen.

Abdomen pale yellow to dark brown. In males ninth tergum and basistyles brown. In males lobes of ninth tergum in lateral view (Fig. 33) broad, not extending beyond apices of basistyles, lobe apices pointed; in dorsal view (Fig. 34) lobes thick, diverging apically, with 30 or more black spines across apical halves of lobes. Basistyles broad. Dististyles short, acute. Aedeagus with distinctive bilobed base (penunci), tapering apically to slender coiled thread. Cerci elongate, slender, extending slightly beyond apices of basistyles.

This species is similar to *B. punctiger* in having wings with an apical crossvein and margined crossveins although it differs markedly from *B. punctiger* in characters of the ninth tergum in males and the lack of a dark brown spot surrounding the base of each femoral seta.

This species is the strongest flier of the midwestern bittacids and has been collected from damp, cool, shaded bottomlands and dry, shaded hillsides. In moist areas it is associated with jewelweed and stinging wood nettle, while in drier areas it has been collected frequently on gooseberry and multiflora rose.

This species extends from Florida to Canada and west to Minnesota and Kansas (Fig. 45).



Fig. 45.—Distribution of *Bittacus pilicornis* in Illinois and North America.

Illinois Records.—(Fig. 45). Collected in Illinois from June to mid-August.

Bittacus occidentis Walker

Bittacus occidentis Walker (1853:469).
♂, ♀. Type-locality: Erie, United States. Type-specimen missing.

Bittacus arizonicus Banks (1911:350).
♂. Type-locality: Palmerlee, Arizona. Synonymized by Carpenter (1931a).

Head and thorax dark yellowish brown to dark brown.

Wings (Fig. 25) pale yellow, pterostigma slightly darker than surrounding membranes. Subcostal crossvein distal to first fork of radial sector. Two pterostigmal crossveins. Apical crossveins

absent. Several specimens possess an apical crossvein on at least one of the fore wings. In one specimen the subcostal crossvein occurs at the first fork of the radial sector although this crossvein is normally found well beyond the fork.

Legs yellowish brown to brown, apices of tibiae dark brown. Hind femora swollen.

Abdomen yellowish brown to brown. In males ninth tergum and basistyles yellowish brown to dark brown. Ninth tergum in lateral view (Fig. 35) narrow, rounded apically, extending to or slightly beyond apices of basistyles; in dorsal view (Fig. 36) ninth tergum diverges apically, with 30 or more black spines along dorsal margins of lobes. Basistyles broad, curved dorsally. Dististyles elongate, narrow. Aedeagus very thick at base, tapered apically to slender thread which curves anteriorly. Cerci short, slender, not extending beyond middle of basistyles.

The wing's subcostal crossvein, distal to the first fork of the radial sector, and the swollen hind femur readily distinguish this species from other Nearctic bittacids.

No specific habitat has been recorded for *B. occidentis*. All Illinois specimens were collected at lights or in light traps.

This species extends from Alabama north into Canada and west to Kansas and Arizona (Fig. 46), with an isolated record from western North Dakota.



Fig. 46.—Distribution of *Bittacus occidentis* in North America.

Illinois Records.—Collected infrequently and in small numbers from mid-July to the end of September. ADAMS COUNTY: Quincy, Evers and Mills, 9-IX-1951, 2 ♂, 2 ♀; Flint, 19-IX-1912, 1 ♂. CHAMPAIGN COUNTY: Champaign, Hart, 18-VII-1889, 1 ♂; Hart, 22-VII-1889, 1 ♀, 1 ♀; Urbana, 18-IX-1909, 1 ♂; Riegel, 19-VII-1938, 1 ♂; Riegel, 29-VIII-1938, 1 ♂; Woodworth, 12-IX-1898, 2 ♂, 4 ♀, 1 ♀; Hart and Kahl, 22-IX-1892, 1 ♀. COLES COUNTY: Charleston, Riegel, 12-IX-1961, 1 ♀. COOK COUNTY: Chicago, W. J. Gerhard, 6-IX, 23-VII, 6 ♂, 1 ♀. McDONOUGH COUNTY: Macomb, 25-IX-1959, 1 ♂. SANGAMON COUNTY: Springfield, Frison, 16-IX-1932, 1 ♂, 2 ♀.

Bittacus strigosus Hagen

Bittacus strigosus Hagen (1861:246).
♂, ♀. Type-locality: Chicago, Washington, St. Louis.

Head, thorax, and mouthparts dark yellow to dark brown.

Wings (Fig. 26) clear, pterostigma pale brown, crossveins margined. Subcostal crossvein basal to first fork of radial sector. Two pterostigmal crossveins. Apical crossvein absent.

Legs pale yellow. Hind femora cylindrical.

Abdomen dark yellow to dark brown. In males ninth tergum and basistyles brown. In males lobes of ninth tergum in lateral view (Fig. 37) broad basally, narrowed apically, apices of lobes rounded, extending well beyond apices of basistyles and having elongate medial prominences on ventral margins with several long black setae and spines; in dorsal view (Fig. 38) lobes broad basally, apical third constricted, converging medially at apex. Basistyles broad. Dististyles broad, elongate. Aedeagus thickened basally, extended apically in form of thin, tightly coiled thread. Cerci narrow, elongate, extending well beyond apices of basistyles, bases of cerci enlarged.

This species has margined crossveins like those of *B. pilicornis* and *B. puncti-*

ger but lacks the apical crossvein. The lobes of the ninth tergum in dorsal view readily separate the males from other midwestern bittacid males.

B. strigosus is found abundantly in Illinois in habitats ranging from moist shaded bottomlands to dry pastures. This species can be collected on a wide range of plants.

B. strigosus extends from Louisiana and South Carolina to Canada and west to Manitoba and Montana (Fig. 47).



Fig. 47.—Distribution of *Bittacus strigosus* in Illinois and North America.

Illinois Records.—(Fig. 47). Collected from early June to early September in almost every county in Illinois.

Bittacus stigmaterus Say

Bittacus stigmaterus Say (1823:164).

Type-locality: Fort Osage, Missouri.

Type-specimen missing.

Bittacus pallidipennis Westwood (1846:195). ♂. Type-locality unknown. Synonymized by Hagen (1861).

Head and thorax yellow to dark brown.

Wings (Fig. 27) amber, pterostigma slightly darker than surrounding area, crossveins not margined except in specimens found in western areas of Missouri and Arkansas. Subcostal crossvein basal to first fork of radial sector. Two pterostigmal crossveins. Apical crossvein absent.

In almost all specimens examined the wings were uniformly colored, and the crossveins were not margined although specimens collected in southwestern Missouri and Arkansas show some margination of the crossveins.

Legs dark yellowish brown. Femora slightly swollen.

Abdomen pale yellow to dark brown. In males ninth tergum and basistyles brown. In males lobes of ninth tergum in lateral view (Fig. 39) narrow, subrectangular, extending well beyond apices of basistyles; in dorsal view (Fig. 40) lobes converge apically, with two distinct medial prominences on each lobe, each prominence with several black spines; a small patch of spines present near ventral margin of lobes. Basistyles broad. Dististyles short, rounded apically. Aedeagus thickened basally, tapered apically. Cerci narrow, elongate, extending beyond apices of basistyles.

This species closely resembles *B. texanus*. The females are separated on the basis of wing color, which is not always reliable. In places where these two species overlap, the wing crossveins in *B. stigmaterus* are often margined. The males of these two species can be separated by the arrangement of spines on the medial margin of the ninth tergum.

This species has been collected in habitats similar to those of *B. strigosus* and *B. apicalis* although it is sometimes found in fairly dry woods.

B. stigmaterus extends from Georgia to New York and west to Minnesota and Texas (Fig. 48).



Fig. 48.—Distribution of *Bittacus stigmaterus* in Illinois and North America.

Illinois Records.—(Fig. 48). Collected from late June to mid-September.

Bittacus texanus Banks

Bittacus texanus Banks (1908:261). ♂.
Type-locality: Plano, Texas.

Head and thorax dark reddish brown.

Wings (Fig. 28) pale brown, pterostigma concolor with membranes, crossveins not margined. Subcostal crossvein basal to first fork of radial sector. Two pterostigmal crossveins. Apical crossvein absent.

Legs dark reddish brown. Hind femora slightly swollen.

Abdomen and terminalia dark reddish brown. In males lobes of ninth tergum in lateral view (Fig. 41) narrow, elongate, extending well beyond apices of basistyles; in dorsal view (Fig. 42) lobes converge apically, medial margin having a prominence bearing several short, thick spines; 10–15

short, thick spines present along medial margin basal to this prominence, three to four short and thick medial spines occur near apices of lobes. Basistyles broad. Dististyles short, globular. Aedeagus thickened basally, tapered apically to fine thread. Cerci narrow, elongate, extending well beyond apices of basistyles.

B. texanus closely resembles *B. stigmaterus* although *B. texanus* is much darker in color. The females are separated on the basis of wing color, which, as already noted, is not always reliable. The males of these two species can be separated by the arrangement of spines on the medial margin of the ninth tergum.

Little is known of the habitat of this species. In Texas individuals were collected with *B. stigmaterus* along streams under cover of willows and elms.

B. texanus has been recorded from Texas, Florida, Kansas, and New Mexico (Fig. 49).

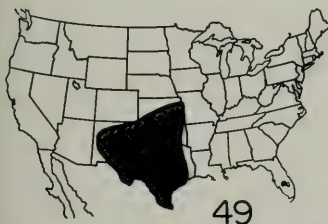


Fig. 49.—Distribution of *Bittacus texanus* in North America.

BOREIDAE Stephens 1829

The Boreidae are winter insects, the adults emerging from November until May. Adults and scarabaeiform larvae live in, and feed on, moss. The small size of these insects (varying in length from 2.5 to 5.0 mm), the presence of rudimentary wings, and the distinct ovipositor in females readily define this family of Mecoptera. The family

Boreidae has only one genus, *Boreus*, which occurs in Europe, Asia, and North America. Fifteen species are recorded from North America, but only two species occur east of the Rocky Mountains.

Boreus Latreille

Boreus Latreille (1816:152). Type-species: *Boreus hyemalis* Linnaeus. *Euboreus* Lestage (1940:12). Synonymized by Cooper (1972).

Ateleptera Dalman (1823:34). Synonymized by Esben-Petersen (1921).

Small, stout insects. Coloration varies from reddish in *B. elegans* to olive green in some specimens of *B. brevicaudus* to brown and black in most species. Length 2.5–5.0 mm. Head broad, tapered apically to long rostrum. Ocelli present, but difficult to see. Compound eyes black, oval. Antennae brown to black, filiform, with 18–24 flagellar segments.

Thorax reddish brown to olive to black. Pronotum broad, collarlike, anterior margin smooth, rounded. Wings light brown to black. In males wings reduced to pair of thick, chitinous, coreaceous rudiments, broad basally, tapering apically to acute point, with coarse lateral and medial setae. Hind wings thin, membranous, covered by fore wings. In females fore wings reduced to short, oval pads covering hind wing pads, except for extremely reduced wing pads of *B. reductus*. Legs dark yellow to black, elongate, with simple claws.

Abdomen short, thick, pale brown to black. In males ninth tergum short, broad, apex truncate or emarginate, with numerous short black spines; in some species a concave medial depression receives apices of dististyles. Ninth sternum (hypandrium) broad, rounded; apex rounded, truncate, or emarginate. Basistyles thick, broad. Dististyles narrow, elongate, each with mesal lobe and several thick spines along dorsal margin. In females ovipositor composed of

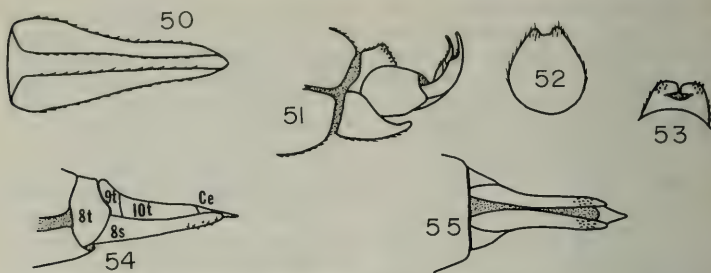


Fig. 50-55.—*Boreus brumalis*. 50.—Dorsal view of male fore wing. 51.—Lateral view of male terminalia. 52.—Ventral view of male ninth sternum (hypandrium). 53.—Dorsal view of male ninth tergum. 54.—Lateral view of female ovipositor. 8t, eighth tergum. 8s, eighth sternum. 9t, ninth tergum. 10t, tenth tergum. Ce, cerci. 55.—Ventral view of female ovipositor.

eighth through tenth segments and cerci. Eighth sternum formed by two elongate sclerotized plates. Tenth tergum subrectangular, elongate, apex emarginate. Cerci short, triangular, apex acute. Eleventh segment hidden beneath cerci.

Only one species of *Boreus* occurs in Illinois.

KEY TO THE MIDWESTERN SPECIES OF BOREUS

MALES

1. Specimens pale to dark reddish brown. Fore wing curved smoothly to apex (Fig. 57). Ninth sternum (Fig. 59) rounded apically. Ninth tergum (Fig. 60) rounded apically *nivoriundus*

Specimens dark brown to black. Fore wing constricted near middle (Fig. 50). Ninth sternum (Fig. 52) emarginate apically. Ninth tergum (Fig. 53) with medial fissure *brumalis*

FEMALES

1. Specimens pale to dark reddish brown. Ovipositor 1.20 mm in length (measured from base of eighth sternum to apices of cerci) *nivoriundus*

Specimens dark brown to black. Ovipositor 0.53 mm in length *brumalis*

Boreus brumalis Fitch

Boreus brumalis Fitch (1847:278). ♂, ♀. Type-locality: eastern New York.

Head and thorax dark brown to black.

Fore wings (Fig. 50) in males dark brown to black, slender, apical half narrowed, apex acute with numerous coarse black setae along lateral and medial margins. Hind wings with single apical spur. Fore wings of females dark brown to black, rudimentary, reduced to small suboval pads.

Legs elongate, dark brown to black.

Abdomen and terminalia (Fig. 51) dark brown to black. In males ninth tergum (Fig. 53) short, broad basally, apex truncate with narrow medial fissure, lateral areas of apex with numerous short black spines; shallow medial depression receives tips of dististyles. Dististyles elongate, curved dorsally, apices acute; numerous small spines along dorsal margins of the dististyles, with narrow elongate lobes on mesal margins. At rest dististyles curve dorsally to fit into dorsomedial depression of ninth tergum. Ninth sternum (hypandrium) oval, apical margin emarginate (Fig. 52). In ventral view (Fig. 55) eighth sternum of female formed by two narrow, elongate plates, 6.0 times longer than wide, rounded apically, with numerous short apical spines, bases and apices separated. In lateral view (Fig. 54) eighth sternum broad basally, apical three-fourths thick, extending beyond apex of tenth tergum. Tenth tergum elongate, thick,

3.6 times longer than wide. Tenth sternum hidden. Cerci short, triangular, apices acute.

This species is related to *B. nivoriundus*, the other eastern North American species of *Boreus*. The dark brown to black coloring generally separates *B. brumalis* from *B. nivoriundus* in addition to the constricted wing pads and emarginate apical margin of the ninth sternum (hypandrium) in males.

In Illinois individuals of *B. brumalis* have been collected primarily on moss in the beach-maple-tulip forest of southwestern Illinois along the escarpment of the Mississippi River.

B. brumalis extends from Tennessee to Massachusetts and west to Ohio and Michigan with isolated populations in Illinois, Wisconsin, and Minnesota (Fig. 56).

Illinois Records.—(Fig. 56). The first record of *Boreus* in Illinois was re-

ported from Fountain Bluff in Jackson County by Stannard (1957). Individuals have since been collected from mid-October to mid-April only in the Ozark uplift of Illinois.

Boreus nivoriundus Fitch

Boreus nivoriundus Fitch (1847:277).

♂, ♀. Type-locality: eastern New York.

Head and thorax light to dark reddish brown.

Fore wings in males (Fig. 57) pale brown, broad basally, tapering apically, with numerous strong black setae along lateral and medial margins. Hind wings with single apical spur. In females fore wings pale brown, rudimentary, reduced to small suboval pads.

Legs elongate, pale brown.

Abdomen and terminalia (Fig. 58) pale brown. In male ninth tergum (Fig. 60) short, broad basally, apex broadly rounded, with numerous short, black spines; medial depression receives apices of dististyles. Dististyles elongate, curved dorsally, apex acute, dorsal margin with numerous small dark spines; at rest dististyles curved dorsally to rest in dorsomedial depression of ninth tergite. Ninth sternum (hypandrium) broad, entire, oval, rounded apically (Fig. 59). In ventral view (Fig. 62) eighth sternum of female formed by two narrow, elongate plates, 6.3 times longer than wide, rounded apically, with numerous short, apical spines, bases and apices of plates separated. In lateral view (Fig. 61) eighth sternum broad basally, apical three-fourths flattened dorsoventrally, extending beyond apex of tenth tergum. Tenth tergum elongate, thick, 3.1 times longer than wide. Cerci short, fused, triangular, apex acute. Tenth and eleventh sterna hidden.

B. nivoriundus is one of two eastern species and differs from *B. brumalis* in its pale to reddish brown coloration, the longer length of the female ovipositor, and the rounded apices of the ninth tergum and sternum in males.



Fig. 56.—Distribution of *Boreus brumalis* in Illinois and North America.

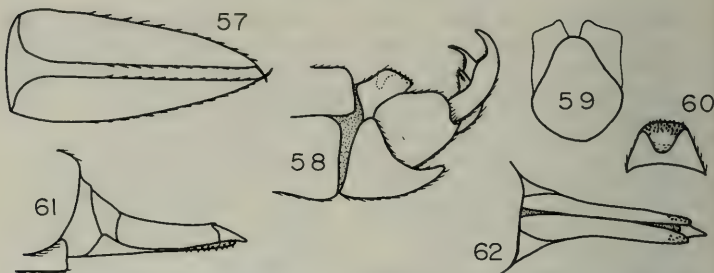


Fig. 57-62.—*Boreus nivoriundus*. 57.—Dorsal view of male fore wing. 58.—Lateral view of male terminalia. 59.—Ventral view of male ninth sternum (hypandrium). 60.—Dorsal view of ninth tergum of male. 61.—Lateral view of female ovipositor. 62.—Dorsal view of female ovipositor.

Often collected with *B. brumalis* in the deciduous forests of eastern North America.

B. nivoriundus extends from Massachusetts to Maine and southwest through New York and on to Ohio, Kentucky, and Tennessee (Fig. 63).



Fig. 63.—Distribution of *Boreus nivoriundus* in North America.

MEROPEIDAE Esben-Petersen 1921

This family name is emended from Meropidae Esben-Petersen (1921) by Opinion 140 of the International Commission of Zoological Nomenclature.

The family Meropeidae is the most primitive group of extant Mecoptera in North America. The broadly rounded wings with their dense venation associate the Meropeidae with the South American family Notiothaumidae although current knowledge of morphol-

ogy (Mikoleit 1971a) indicates that these two families are not as closely related as was previously thought. The Meropeidae differ from the Notiothaumidae in the absence of ocelli, the non-coalescing radial and medial veins at the bases of the wings, and the absence of a notal organ.

Two genera are recorded for the Meropeidae. *Merope* is found in eastern and north-central North America, and *Austromerope* in western Australia.

Merope Newman

Merope Newman (1838:180). Type-species: *Merope tuber* Newman by monotypy. The description of the type-species will characterize the genus.

Merope tuber Newman

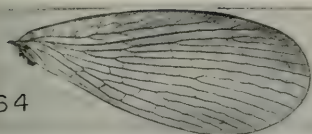
Merope tuber Newman (1838:180). ♀, ♂. Type-locality: Trenton Falls, New York.

Head pale yellow to brown. Ocelli absent.

Thorax pale yellow to pale brown. Pronotum shieldlike, extending anteriorly over vertex of head, with distinct dorsomesal suture.

Fore wing length 11.0–13.0 mm. Membranes (Fig. 64) pale whitish yellow; wing broad, apex rounded. Costa circumambient, broader along anterior

64

Fig. 64.—*Merope tuber* fore wing.

margin. Veins and crossveins numerous and variable. Pterostigma not distinct. Thyridium absent. Small brown basal lobe near apex of A_2 . Hind wings slightly smaller than fore wings. The fore wings contain numerous veins and crossveins which show considerable variation in their number, branching, and origins.

Legs pale yellow. Tarsal claws paired, simple.

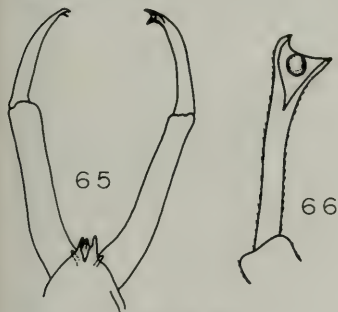
Abdomen pale yellow to brown, segments subrectangular, flattened dorsoventrally. Male terminalia (Fig. 65) pale yellow, elongate, equal in length to or longer than abdomen. Ninth tergum short, emarginate apically, forming two pointed lobes. Anus mesoventrally beneath ninth tergum. Basistyles elongate, broad basally. Dististyles elongate, shorter than basistyles, apex of each dististyle flattened laterally, emarginate, forming two black clawlike lobes; small apical concave disc in mesal margin of each dististyle (Fig. 66). Cerci present as short clavate

lobes posterior to ninth tergum. Female terminalia lack sclerotized genital bulb.

Specimens of *M. tuber* are rare in collections but have been collected from a variety of habitats. Illinois specimens have been collected in Malaise and picric acid traps. Indiana specimens have been collected by bait traps in a hickory woods near Lafayette. Most specimens recorded have been taken at lights, under stones, in rotting logs, and in European chafer traps. *Merope* appears to spend a great deal of time on the ground.

Nothing is known of the immature stages of this insect.

M. tuber extends from northern Georgia to Maine and west to Missouri and Minnesota (Fig. 67).

Fig. 67.—Distribution of *Merope tuber* in North America.Fig. 65-66.—*Merope tuber*. 65.—Dorsal view of male terminalia. 66.—Male dististyle.

Illinois Records.—Collected during August in southern Illinois and during May in east-central Illinois. CHAMPAIGN COUNTY: Urbana, Trelease Woods, K. H. Leim, 1-7-V-1972, 1 ♀. UNION COUNTY: Pine Hills, H. S. Dybas, 28-VIII-1963, 29-VIII-1963, 5-VIII-1963, 2 ♂, 4 ♀.

PANORPODIDAE Issiki 1933

Byers (1965) first used the family name Panorpodidae but has recommended that Issiki (1933) be credited with the name because Issiki first suggested that the genus *Panorpodes* be raised to subfamily rank.

The short rostrum of *Brachypanorpa* with the gena bearing a distinct tooth separates the panorpidids from other families of North American Mecoptera. Two genera are distinguished, with *Panorpodes* restricted to eastern Asia and *Brachypanorpa* found in southeastern and northwestern North America. The family Panorpididae is very closely associated taxonomically with Panorpididae, and Byers (1965) erected the family Panorpididae on the basis of their being phytophagous and because of the differences between the larvae of the two groups.

Only *Brachypanorpa* occurs in North America, but this genus does not occur in the Midwest.

Brachypanorpa Carpenter

Brachypanorpa Carpenter (1931a:209).

Type-species: *Panorpodes carolinensis* Banks.

Three ocelli present. Antennae filiform, 30-40 flagellar segments, genae with distinct acute lobes. Thorax yellowish brown. Wings yellowish brown to amber, crossveins not margined. Pterostigma concolor with rest of wing. Thyridium absent. Wings reduced in some females. Legs elongate, dark yellowish brown, with pair of simple claws. Body light yellowish brown. Abdomen and terminalia dark yellowish brown, oval. Ninth tergum of males oval, emarginate apically, forming two thick lateral lobes. Hypoalves thick, fused near middles of basistyles, separate apically. Basistyles oval, elongate, longer than dististyles.

Three species of *Brachypanorpa* are recorded from North America: *B. carolinensis* in the southern Appalachians and *B. oregonensis* and *B. montana* in the northwestern states (Fig. 13).

PANORPIDAE Stephens 1835

The paired, serrate claws; the elongate rostrum; the presence of a thyridium; and the narrow, elongate wings with the cubital vein not fused to the

medial vein separate the panorpidids from other families of Mecoptera. Three genera are recognized. *Leptopanorpa* and *Neopanorpa* are found in Asia, and *Panorpa* occurs in North America and Eurasia.

In North America *Panorpa* contains the greatest number of species of any genus of Mecoptera. Twenty-three species occur in the Midwest, eight in Illinois.

Panorpa Linnaeus

Panorpa Linnaeus (1758:551). Type-species: *Panorpa communis* Linnaeus.

Aulops Enderlein (1910:390). Synonymized by Esben-Petersen (1915).

Estenalla Navás (1912:356). Synonymized by Esben-Petersen (1915).

Head pale yellow to dark reddish brown. Ocelli amber on raised subtriangular pad. Antennae filiform with more than 30 flagellar segments. Rostrum elongate, tapered. Mandibles large, heavily sclerotized, with two or three lateral teeth. Labial and maxillary palps have two and four segments, respectively.

Thorax pale yellow to dark reddish brown. Wings colorless to amber, crossveins often margined. Membranes patterned with dark brown spots or bands. Thyridium at base of first fork of medial vein. Legs pale yellow to dark reddish brown, with serrate claws.

Abdomen and terminalia yellow to dark reddish brown. The sixth abdominal tergum of males may possess an anal horn. Apex of tergum in males tapered, truncate, or emarginate. Hypoalves generally fused near bases of basistyles except in *lugubris* group. Basistyles broad, oval, usually longer than dististyles. Dististyles simple or with large mesal lobes. Ventral parameres variable. In females the genital plate, usually heavily sclerotized, consists of a distal plate, often a basal plate, and a medial spermathecal apodeme.

KEY TO MIDWESTERN SPECIES
OF PANORPA

MALES (Modified from Carpenter 1931a)

1. Hypovalues fused near middles of
basistyles (Fig. 91)

.....(*lugubris* group) *nuptialis*Hypovalues long, fused near bases of
basistyles (Fig. 93)

2. Anal horn absent

Anal horn (Fig. 20) present

Fig. 68-79.—*Panorpa* fore wings. 68.—*P. nuptialis*. 69.—*P. maculosa*. 70.—*P. submaculosa*. 71.—*P. latipennis*. 72.—*P. acuta*. 73.—*P. banksi*. 74.—*P. sigmoides*. 75.—*P. nebulosa*. 76.—*P. mirabilis*. 77.—*P. galerita*. 78.—*P. hungerfordi*. 79.—*P. subfurcata*.

3. Aedeagus extending posteriorly between dististyles (Fig. 93) 4
 Aedeagus not extending posteriorly between dististyles 5

4. Dististyles slender, smoothly curved (Fig. 93) maculosa
 Dististyles broad, falcate apically (Fig. 95) submaculosa

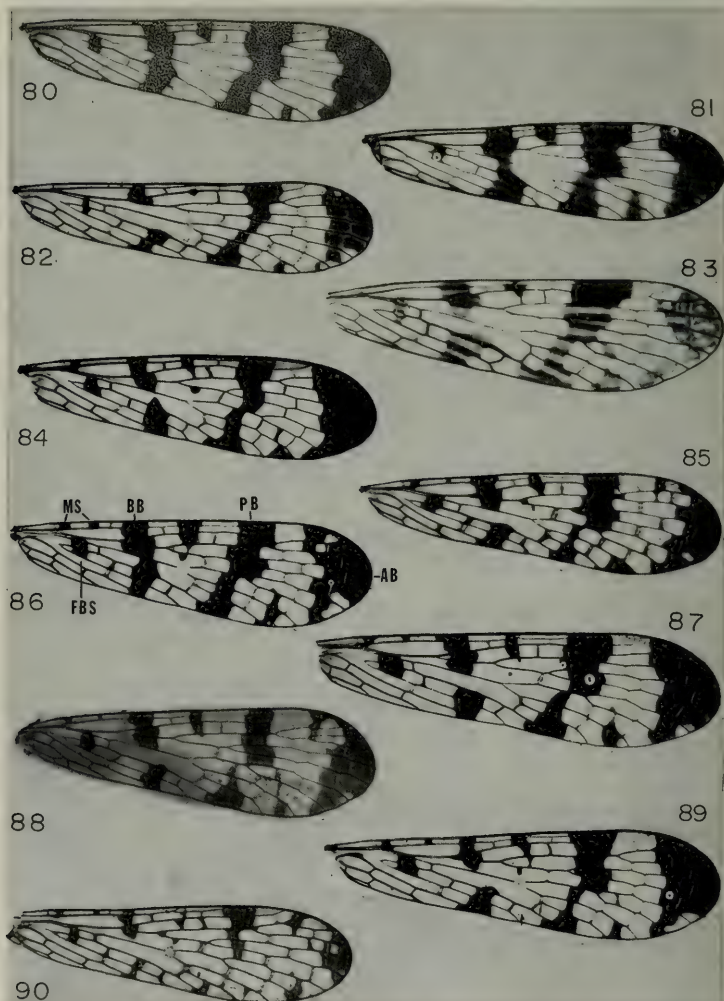


Fig. 80-90.—*Panorpa* fore wings. 80.—*P. helena*. 81.—*P. insolens*. 82.—*P. debilis*. 83.—*P. claripennis*. 84.—*P. rufescens*. 85.—*P. dubitans*. 86.—*P. braueri*. MS, marginal spots. BB, basal band. PB, pterostigmal band. AB, apical band. FBS, first basal spot. 87.—*P. speciosa*. 88.—*P. bifida*. 89.—*P. anomala*. 90.—*P. consuetudinis*.

5. Dististyles with small fingerlike lobe (Fig. 98) *latipennis*

Dististyles simple, without lobes (Fig. 101) 6

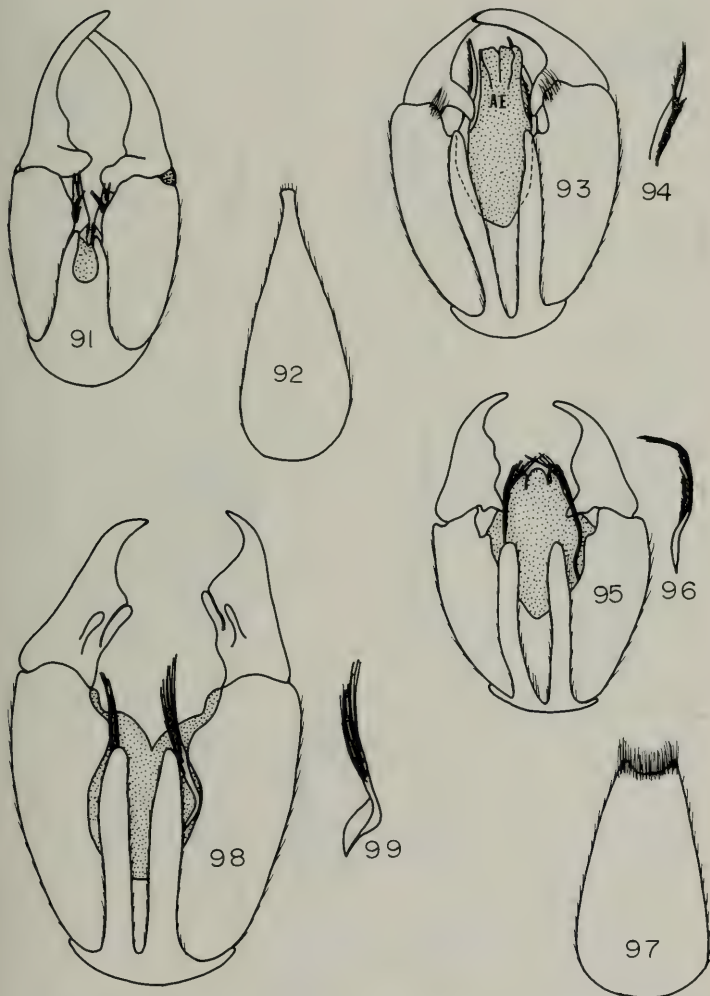


Fig. 91-99.—*Panorpa* male terminalia. 91.—*P. nuptialis*. Ventral view of terminalia. 92.—Dorsal view of ninth tergum. 93.—*P. maculosa*. Ventral view of terminalia. AE, aedeagus. 94.—Ventral paramere. 95.—*P. submaculosa*. Ventral view of terminalia. 96.—Ventral paramere. 97.—Dorsal view of ninth tergum. 98.—*P. latipennis*. Ventral view of terminalia. 99.—Ventral paramere.

6. Ninth tergum truncate apically (Fig. 100) *acuta* 7. Ventral parameres slender, straight (Fig. 105) *banksi*
Ninth tergum emarginate apically (Fig. 103) *banksi*

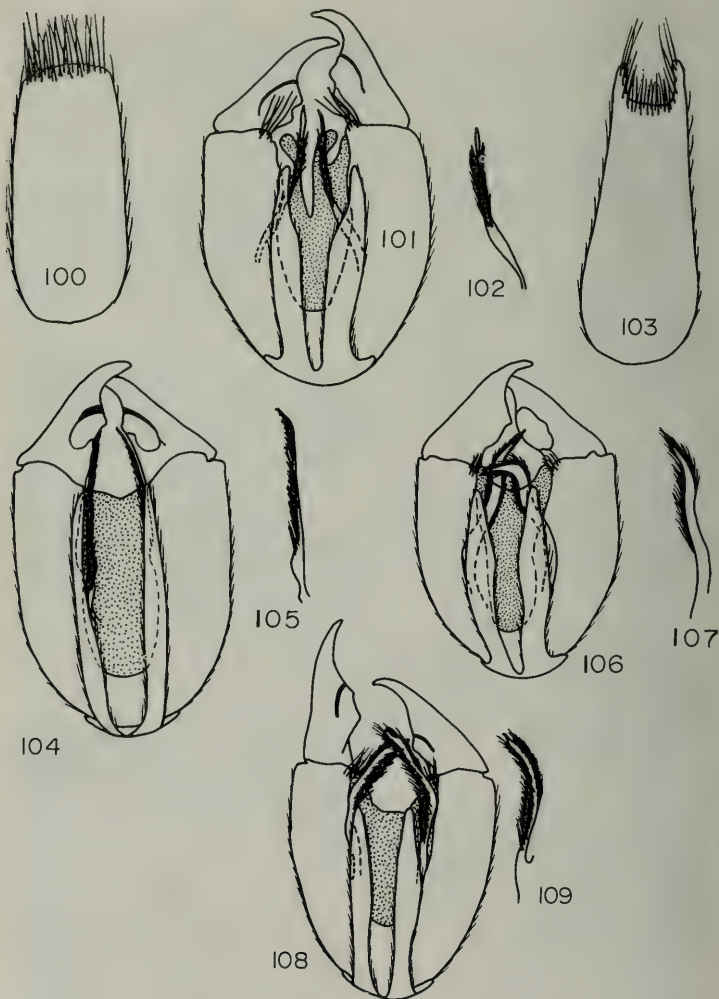


Fig. 100-109.—*Panorpa* male terminalia. 100.—*P. acuta*. Dorsal view of ninth tergum. 101.—Ventral view of terminalia. 102.—Ventral paramere. 103.—*P. banksi*. Dorsal view of ninth tergum. 104.—Ventral view of terminalia. 105.—Ventral paramere. 106.—*P. sigmoides*. Ventral view of terminalia. 107.—Ventral paramere. 108.—*P. nebulosa*. Ventral view of terminalia. 109.—Ventral paramere.

- Ventral parameres thick, curved medially (Fig. 107) 8
8. Ventral parameres sigmoidally curved, with barbs covering apices (Fig. 107) *sigmoides*
- Ventral parameres not sigmoidally curved, with apices constricted and bare (Fig. 109). A small patch of setae on tubercle near bases of dististyles *nebulosa*
9. Dististyles with large lobes (Fig. 115) 10
- Dististyles simple, without lobes (Fig. 120) 13
10. Hypovalves thick, divergent apically (Fig. 111) 11
- Hypovalves slender, elongate (Fig. 115) 12
11. Lobes of dististyles large, covering all but tips of dististyles (Fig. 111) *mirabilis*
- Lobes of dististyles small (Fig. 113) *galerita*
12. Ventral parameres with barbs (Fig. 119) *hungerfordi*
- Ventral parameres without barbs (Fig. 116) *subfurcata*
13. Ventral parameres unbranched (Fig. 121) 14
- Ventral parameres branched (Fig. 137) 19
14. Each basistyle with one to three dark thick setae near base of each dististyle (Fig. 120) *helena*
- Basistyles without dark thick setae near bases of dististyles 15
15. Hypovalves narrow, reaching to bases of dististyles (Fig. 122).... *rufescens*
- Hypovalves not reaching bases of dististyles 16
16. Ventral parameres with basal tuft of barbs (Fig. 125) 17
- Ventral parameres without basal tuft of barbs (Fig. 129) 18
17. Ventral parameres with apical tuft of barbs (Fig. 125) *dubitans*
- Ventral parameres without apical tuft of barbs (Fig. 127) *insolens*
18. Basistyles with apical tubercle bearing tuft of setae (Fig. 128).... *debilis*
- Basistyles without apical tubercle and setae (Fig. 130) *claripennis*
19. Hypovalves thick (Fig. 132). Ventral parameres as in Fig. 133 and 135 20
- Hypovalves thin (Fig. 140). Ventral parameres as in Fig. 137, 139, and 141 21
20. Basal band of wing broken (Fig. 87) *speciosa*
- Basal band continuous (Fig. 86) *braueri*
21. Ventral parameres (Fig. 136) extending well beyond bases of dististyles *bifida*
- Ventral parameres (Fig. 140) short, reaching at most only slightly beyond bases of dististyles 22
22. Hypovalves very short, not reaching to bases of dististyles (Fig. 140). Ventral parameres (Fig. 141) with thick lateral branch, curved dorsally *anomala*
- Hypovalves long, extending to or slightly beyond bases of dististyles (Fig. 138). Ventral parameres (Fig. 139) with two narrow, thin branches *consuetudinis*
- ### FEMALES
1. Wings with very broad bands (Fig. 68). Apex of genital plate truncate (Fig. 142) *nuptialis*
- Wings with narrow bands or spots (Fig. 73 and 80). Apex of genital plate emarginate 2
2. Pterostigmal band not continuous from anterior to posterior margin of wing (Fig. 73) 3
- (*nebulosa* group) .. 3
- Pterostigmal band continuous from anterior to posterior margin of wing (Fig. 80)..... (*rufescens* group) .. 8
3. Spermathecal apodeme (Fig. 146) extending beyond base of distal plate. Genital plate greater than 1.0 mm in length 5
- Spermathecal apodeme (Fig. 143) not extending beyond base of distal plate. Genital plate less than 1.0 mm in length 4
4. Genital plate (Fig. 143) about 0.44 mm in length; lateral lobes of apical emargination of distal plate moderately broad *maculosa*
- Genital plate (Fig. 144) about 0.57 mm in length; lateral lobes of apical emargination of distal plate narrow *submaculosa*
5. Spermathecal apodeme (Fig. 146) reaches to or beyond apical emargination of distal plate 6
- Spermathecal apodeme (Fig. 145) does not reach apical emargination of distal plate *latipennis*
6. First marginal spot present (Fig. 73). Genital plate (Fig. 146) narrow, elongate, over 1.5 mm in length *banksi*

First marginal spot absent. Genital plate (Fig. 147 and 149) oblong or oval, 1.5 mm or less in length 7

7. Genital plate (Fig. 149) oblong, constricted basally *nebulosa*
acuta

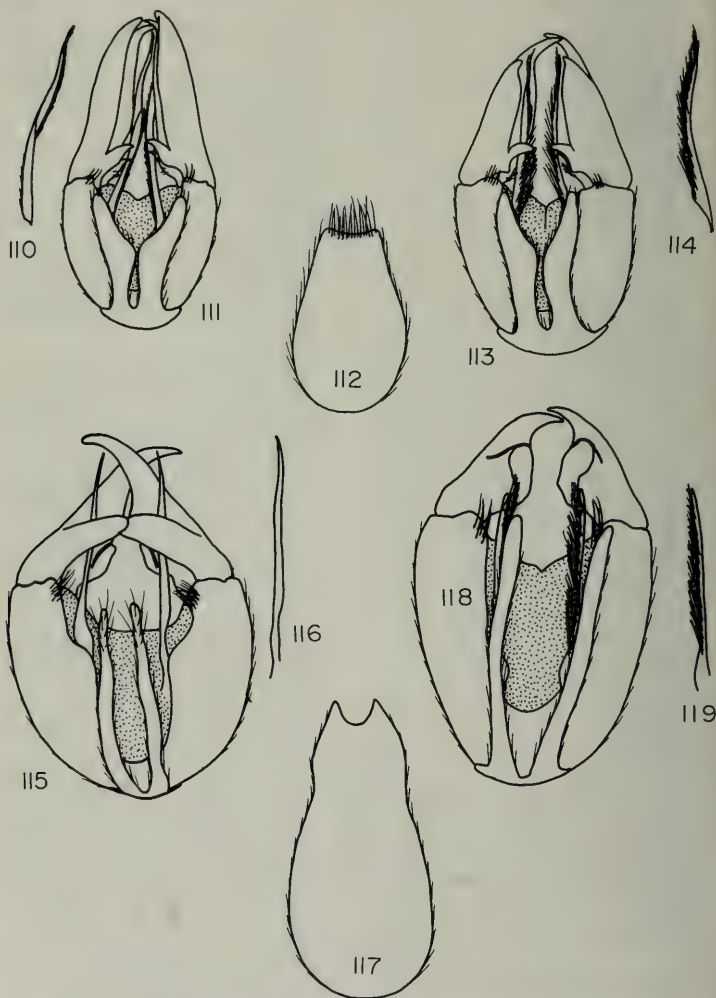


Fig. 110-119.—*Panorpa* male terminalia. 110.—*P. mirabilis*. Ventral paramere. 111.—Ventral view of terminalia. 112.—*P. galerita*. Dorsal view of ninth tergum. 113.—Ventral view of terminalia. 114.—Ventral paramere. 115.—*P. subfurcata*. Ventral view of terminalia. 116.—Ventral paramere. 117.—Dorsal view of ninth tergum. 118.—*P. hungerfordi*. Ventral view of terminalia. 119.—Ventral paramere.

Genital plate (Fig. 147) oval, basal
two-thirds of plate broad ...sigmoides

8. Marginal spot(s) present 9
Marginal spot(s) absent 16

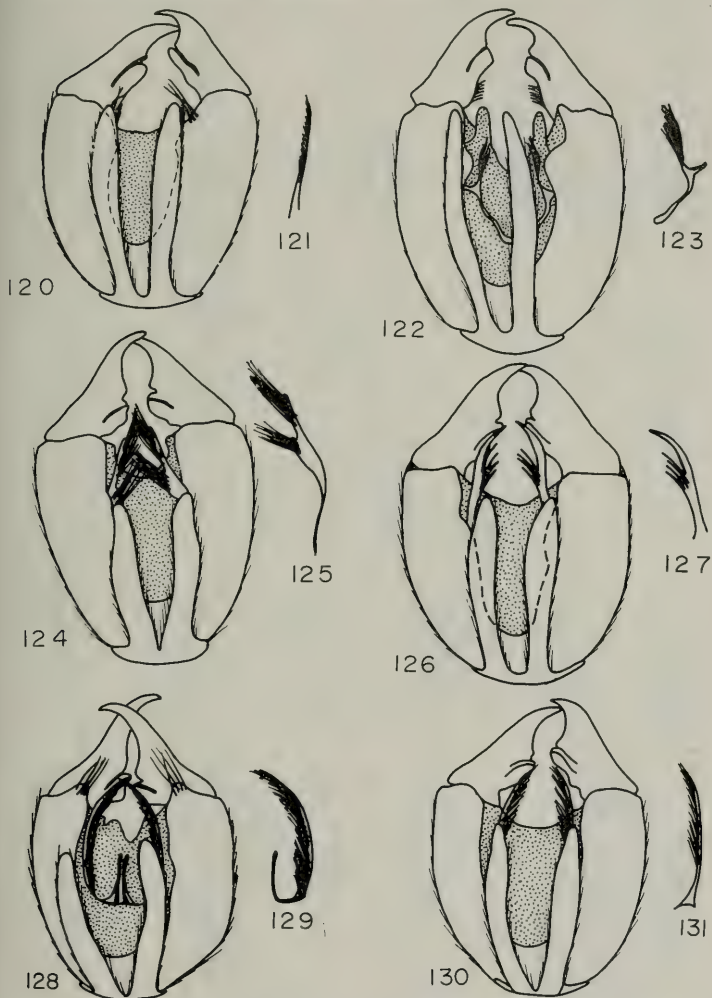


Fig. 120-131.—*Panorpa* male terminalia. 120.—*P. helena*. Ventral view of terminalia. 121.—Ventral paramere. 122.—*P. rufescens*. Ventral view of terminalia. 123.—Ventral paramere. 124.—*P. dubitans*. Ventral view of terminalia. 125.—Ventral paramere. 126.—*P. insolens*. Ventral view of terminalia. 127.—Ventral paramere. 128.—*P. debilis*. Ventral view of terminalia. 129.—Ventral paramere. 130.—*P. claripennis*. Ventral view of terminalia. 131.—Ventral paramere.

9. Spermathecal apodeme extends beyond base of distal plate one or more times length of plate (Fig.

164) 10
Spermathecal apodeme extends beyond base of distal plate by less than

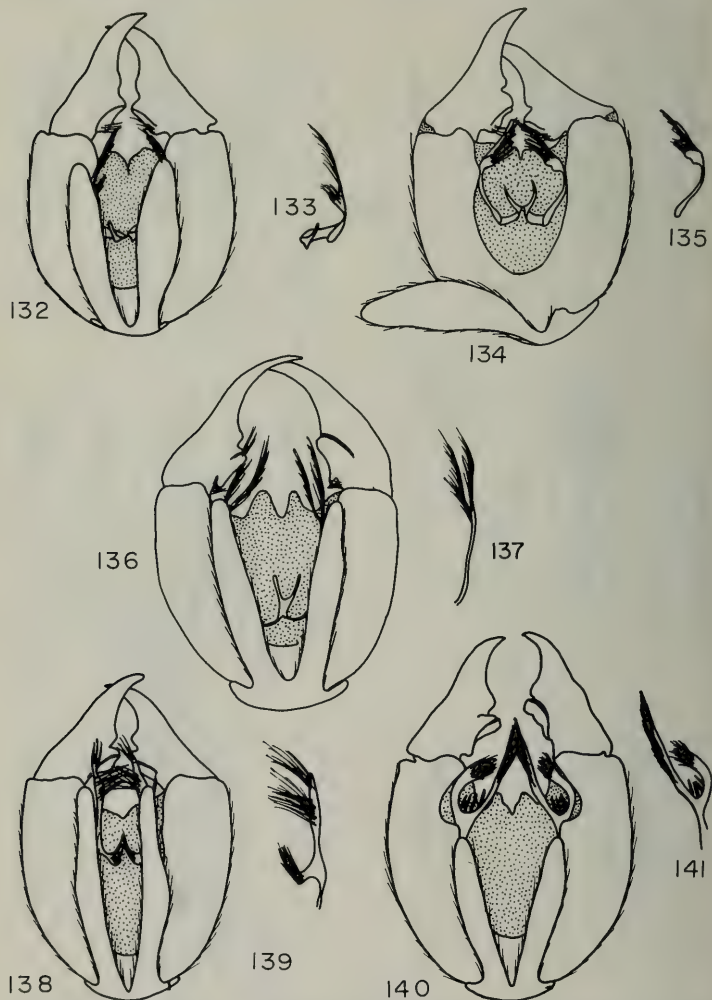


Fig. 132-141.—*Panorpa* male terminalia. 132.—*P. speciosa*. Ventral view of terminalia. 133.—Ventral paramere. 134.—*P. braueri*. Ventral view of terminalia. 135.—Ventral paramere. 136.—*P. bifida*. Ventral view of terminalia. 137.—Ventral paramere. 138.—*P. consuetudinis*. Ventral view of terminalia. 139.—Ventral paramere. 140.—*P. anomala*. Ventral view of terminalia. 141.—Ventral paramere.

length of plate (Fig. 160) 12

rectangular basal membrane

10. Genital plate (Fig. 164) with sub-

..... consuetudinis

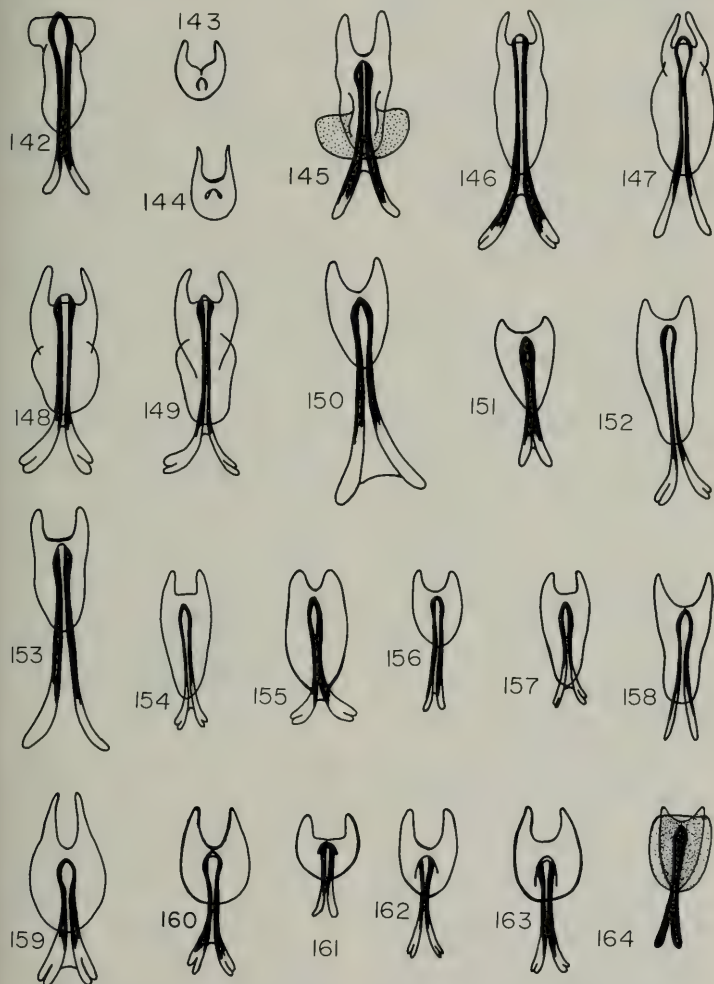


Fig. 142-164.—Female genital plate. 142.—*Panorpa nuptialis*. 143.—*Panorpa maculosa*. 144.—*Panorpa submaculosa*. 145.—*Panorpa latipennis*. 146.—*Panorpa banksi*. 147.—*Panorpa sigmoides*. 148.—*Panorpa acuta*. 149.—*Panorpa nebulosa*. 150.—*Panorpa mirabilis*. 151.—*Panorpa galerita*. 152.—*Panorpa hungerfordi*. 153.—*Panorpa subfurcata*. 154.—*Panorpa helena*. 155.—*Panorpa rufescens*. 156.—*Panorpa dubitans*. 157.—*Panorpa insolens*. 158.—*Panorpa debilis*. 159.—*Panorpa claripennis*. 160.—*Panorpa speciosa*. 161.—*Panorpa braueri*. 162.—*Panorpa bifida*. 163.—*Panorpa anomala*. 164.—*Panorpa consuetudinis*.

- Genital plate without subrectangular basal membrane 11
11. Genital plate (Fig. 156) about 0.85 mm in length *dubitans*
Genital plate (Fig. 153) about 1.76 mm in length *subfurcata*
12. Genital plate (Fig. 161) short, broad, about 0.69 mm in length. Crossveins margined; basal band continuous *braueri*
Genital plate about 1 mm or more in length. Basal band broken 13
13. Genital plate (Fig. 155) about 0.98 mm in length, with lateral lobes of apical emargination short and thick. Distal plate oval. Spermathecal apodeme extends beyond base of distal plate 0.41 times length of plate *rufescens*
Genital plate subcircular. Spermathecal apodeme extends beyond base of distal plate more than 0.60 times length of plate 14
14. Genital plate (Fig. 160) deeply emarginate apically, reaching almost to apex of spermathecal apodeme *speciosa*
Genital plate (Fig. 163) with moderate emargination apically 15
15. Inner margins of apical emargination of genital plate (Fig. 162) parallel. Genital plate about 0.99 mm in length *bifida*
Inner margins of apical emargination of distal plate (Fig. 163) converging. Genital plate about 1.15 mm in length *anomala*
16. Crossveins margined 17
Crossveins not margined 18
17. Genital plate (Fig. 159) very broad basally, over 1 mm in length *claripennis*
Genital plate (Fig. 158) constricted basally, 1 mm or less in length *debilis*
18. Wing membranes colorless 19
Wing membranes pale yellow to amber 21
19. First basal spot fused with anterior part of basal band (Fig. 76) *mirabilis*
First basal spot not fused with basal band 20
20. Genital plate (Fig. 151) with shallow emargination apically, about 0.97 mm in length *galerita*
Genital plate (Fig. 153) deeply emarginate apically, about 1.76 mm in length *subfurcata*
21. Genital plate (Fig. 152) elongate, about 1.50 mm in length *hungerfordi*

- Genital plate less than 1.30 mm in length 22
22. Genital plate (Fig. 154) about 1.07 mm in length *helena*
Genital plate (Fig. 157) about 0.98 mm in length *insolens*

Lugubris Group

The *lugubris* group consists of three Nearctic species, *P. lugubris*, *P. rufa*, and *P. nuptialis*, which are dark reddish brown to black with dark, broad wing bands. The sixth abdominal tergum of males lacks an anal horn. The seventh and eighth abdominal segments are elongate and slender. The ninth tergum of males is tapered apically, and the hypovalves, or ninth sternum, are fused near the mid length of the basistyles.

Panorpa nuptialis Gerstaecker

Panorpa nuptialis Gerstaecker (1863: 187). ♀, ♂. Type-locality: Texas.

Head and thorax reddish brown.

Fore wing length 14.0–17.9 mm.

Membranes (Fig. 68) amber, crossveins not margined. Apical band dark brown, broad, entire. Pterostigmal band dark brown, broad, entire, not forked. Basal band dark brown, broad, entire. Marginal and first basal spots fused. Second basal spot large, extending along posterior margin of wing from base to posterior fourth of basal band.

Legs dark reddish brown.

Abdomen reddish brown. Male terminalia reddish brown. Ninth tergum (Fig. 92) broad and rounded basally, tapering apically to narrow truncate apex. Hypovalves (Fig. 91) broad basally, fused well beyond bases of basistyles, separated apically to form two narrow, lateral lobes, ending well before bases of dististyles. Basistyles large, oval. Dististyles equal in length to basistyles. Ventral parameres narrow, elongate, branched, extending to bases of dististyles. Female genital plate large (Fig. 142), elongate, 1.35 mm in length. Distal plate broadened laterally, apex truncate. Basal plate narrow, elongate. Spermathecal apo-

deme elongate, bifurcate basally, extending slightly beyond apex of distal plate.

The broad dark bands on the wings and the elongate seventh and eighth abdominal segments associate *P. nuptialis* with *P. lugubris* and *P. rufa*. Both sexes of *P. nuptialis* are readily distinguished by the broad, unforked pterostigmal band and the large second basal spot which extends along the posterior margin of the wing from the base to the basal band.

Individuals of *P. nuptialis* have been collected in dense vegetation along a drainage ditch in Missouri, in short grass of roadside ditches, and in cotton and soybean fields. The general habitat of this and other species of the *P. lugubris* group differs markedly from that of most panorpids.

P. nuptialis is a south-central species recorded from Louisiana to Missouri and southwest into Mexico (Fig. 165).



Fig. 165.—Distribution of *Panorpa nuptialis* in North America.

It is the only species of this group to extend up the Mississippi valley, and it has been collected within a mile of Illinois.

Nebulosa Group

The *nebulosa* group consists of eight species of *Panorpa*, seven of which occur in the Midwest. The wing membranes are usually clear, and the wing bands are generally reduced to numerous small spots. In males the sixth abdominal tergum lacks an anal horn.

The seventh and eighth abdominal segments are short. The ninth tergum is truncate or emarginate apically, and the hypovalves are fused at the bases of the basistyles.

Panorpa maculosa Hagen

Panorpa maculosa Hagen (1861:245).

♂, ♀. Type-locality: Pennsylvania.

Panorpa utahensis Gurney (1937:223).

♀ ♀. Synonymized by Gurney (1938), and now placed in *P. submaculosa* by Webb, Penny, and Marlin.

Head and thorax dark to reddish yellow.

Fore wing length 11.6–11.8 mm. Membranes (Fig. 69) clear to pale yellow, crossveins margined. Apical band pale brown, broken into numerous small brown spots. Pterostigmal band broad anteriorly, broken into small brown spots posteriorly. Basal band broken into two small spots. Marginal and second basal spots absent. First basal spot small.

Legs pale to dark yellow.

Abdomen dark yellow to reddish brown. Male terminalia dark yellow. Ninth tergum, as in Fig. 97, oval, broad basally, apex deeply emarginate. Hypovalves (Fig. 93) slender, elongate, ending before bases of dististyles. Basistyles broad, with medial patch of fine setae at bases of dististyles. Dististyles slender, each with large basal lobes, shorter than basistyles. Ventral parameres (Fig. 94) short, slender, unbranched, barbed along one side, extending beyond bases of dististyles. Aedeagus extending between dististyles. Female genital plate (Fig. 143) small, 0.44 mm in length. Distal plate short, rounded basally, apex deeply emarginate, forming two broad lateral lobes. Basal plate absent. Spermathecal apodeme short, not extending beyond base of distal plate and not reaching apical emargination of distal plate.

This species is closely associated with *P. submaculosa*. In both species the

aedeagus extends between the dististyles. In both *P. maculosa* and *P. submaculosa* the female genital plate is small, and the spermathecal apodeme does not extend beyond the base of the distal plate.

Individuals of *P. maculosa* have been collected on tall herbaceous vegetation in swampy woods of ash, oak, and yellow birch (Byers 1954).

P. maculosa extends from Georgia to Vermont and west to Michigan (Fig. 166).

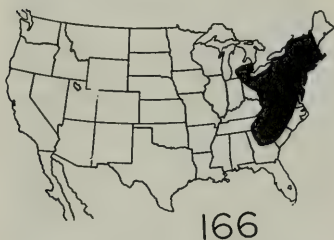


Fig. 166.—Distribution of *Panorpa maculosa* in North America.

Panorpa submaculosa Carpenter

Panorpa submaculosa Carpenter (1931a:255). ♂, ♀. Type-locality: Ann Arbor, Michigan.

Panorpa utahensis Gurney (1937:223). ♂♂. Synonymized by Gurney (1938).

Panorpa utahensis Gurney (1937:223). ♀♀. New synonymy. Gurney (1938) synonymized the females of *P. utahensis* with those of *P. maculosa*.

Head and thorax pale yellow to reddish brown.

Fore wing length 10.4–12.1 mm. Membranes (Fig. 70) clear, crossveins margined. Apical band dark brown, broad, with numerous large clear spots. Pterostigmal band dark brown, broad anteriorly, narrow and broken posteriorly. Basal band broken, forming two small dark brown spots. Marginal and

second basal spots lacking. First basal spot small.

Legs pale to dark yellow.

Abdomen dark yellow to reddish brown. Male terminalia dark yellow. Ninth tergum (Fig. 97) elongate, broad basally, tapered toward emarginate apex. Hypovalues (Fig. 95) moderately broad, extending three-fourths length of basistyles. Basistyles broad. Dististyles short, each with large basi-mesal lobe. Ventral parameres (Fig. 96) narrow, barbed, unbranched, elongate, extending well beyond bases of dististyles. Aedeagus extends posteriorly between dististyles. Female genital plate (Fig. 144) short, 0.57 mm in length. Distal plate short, rounded, deeply emarginate apically, forming two moderately narrow lateral lobes. Basal plate absent. Spermathecal apodeme very short, not extending beyond base of distal plate and not reaching apical emargination of distal plate.

The posterior extension of the aedeagus between the dististyles associates *P. submaculosa* with *P. maculosa*. The two species differ in the shape of the dististyles.

Individuals of *P. submaculosa* are found in drier, less dense habitats than are most species of *Panorpa*.

P. submaculosa is an eastern species, extending from Georgia to Maine and west to Wisconsin (Fig. 167), with an



Fig. 167.—Distribution of *Panorpa submaculosa* in North America.

isolated record from Utah (Gurney 1937, described as *P. utahensis*).

Panorpa latipennis Hine

Panorpa latipennis Hine (1901:248).
♂, ♀. Type-locality: Detroit, Michigan; Sea Cliff, Long Island, New York.

Panorpa longipennis Banks (1911:349).
♀. Type-locality: Black Mountain, North Carolina. Synonymized by Carpenter (1931a).

Head and thorax dark reddish brown.

Fore wing length 13.0–14.0 mm. Membranes (Fig. 71) clear to faint brown, crossveins margined. Apical band pale brown, broken, with numerous clear spots. Pterostigmal band pale brown, broad anteriorly, but broken posteriorly. Basal band reduced to two small pale brown spots. Marginal and second basal spots absent. First basal spot small, pale brown. The continuity of the apical and pterostigmal bands varies considerably. In females the banding is broader and darker than it is in males.

Legs pale brown, apical segments darker.

Abdomen dark reddish brown. Male terminalia reddish brown. Ninth tergum broad, elongate, apex emarginate, forming two broad lateral lobes. Hypovalues (Fig. 98) moderately broad, extending three-fourths length of basistyles, apical one-fourth narrowed. Basistyles broad, longer than dististyles. Dististyles falcate, each with slender fingerlike lobe. Ventral parameres (Fig. 99) narrow, elongate, barbed, unbranched, extending slightly beyond bases of dististyles. Female genital plate (Fig. 145) large, elongate, 1.37 mm in length. Distal plate broad, apex deeply emarginate, forming two broad lateral lobes. Basal plate oval, tapered basally. A broad sclerotized membrane extends laterally over basal plate. Spermathecal apodeme elongate, widely bifurcate basally, not reaching apical emargination of distal plate.

In *P. latipennis* the general appearance of the male terminalia resembles those of *P. banksi* and *P. claripennis* with the fingerlike lobe of each dististyle readily separating *P. latipennis* from these two species.

In Wisconsin individuals have been collected among ferns in a red oak-white pine forest.

P. latipennis is an eastern species which extends from North Carolina to Vermont and west to Michigan and Wisconsin (Fig. 168).

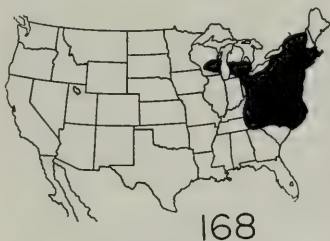


Fig. 168.—Distribution of *Panorpa latipennis* in North America.

Panorpa acuta Carpenter

Panorpa acuta Carpenter (1931a:253).
♂. Type-locality: Smoky Mountains, Tennessee, near Newfound Gap.

Head pale to dark yellow, thorax pale yellow to dark reddish brown.

Fore wing length 10.2–13.4 mm. Membranes (Fig. 72) clear, crossveins margined. Apical band broken into numerous pale brown spots. Pterostigmal band indistinct, broken into numerous pale brown spots. Basal band reduced to two small brown spots. Marginal and second basal spots absent. First basal spot very small, pale brown.

Legs pale yellow.

Abdomen dark yellow to dark reddish brown. Male terminalia dark yellow. Ninth tergum (Fig. 100) narrow, elongate, apex truncate. Hypovalues (Fig. 101) moderately broad, apical

third narrowed, ending before bases of dististyles. Basistyles broad, each with medial patch of thick setae at bases of dististyles. Dististyles shorter than basistyles. Ventral parameres (Fig. 102) narrow, barbed, unbranched, extending slightly beyond bases of dististyles. Female genital plate (Fig. 148) elongate, 1.47 mm in length. Distal plate deeply emarginate apically, forming two moderately broad lateral lobes. Basal lobe narrowed basally. Spermathecal apodeme elongate, extending beyond apical emargination of distal plate.

The truncate ninth tergum of males separates *P. acuta* from other species in the *nebulosa* group although the female genital plate is identical with that of *P. nebulosa*.

P. acuta has been collected in the same habitat as that of *P. nebulosa* along cool shaded ravines and at high elevations.

P. acuta is an eastern species extending from Georgia to Vermont along the Appalachian Mountains with an isolated record from Michigan (Fig. 169).



Fig. 169.—Distribution of *Panorpa acuta* in North America.

Panorpa banksi Hine

Panorpa banksii Hine (1901: 247). ♂.

Type-locality: Sea Cliff, New York.

Panorpa affinis Banks (1895:315). ♂.

Type-locality: Sea Cliff, New York. Original name preoccupied. Renamed by Hine (1901).

Panorpa chelata Carpenter (1931a: 251). ♂, ♀. Type-locality: Wollaston, Massachusetts. Synonymized by Byers (1974).

Head and thorax pale to dark yellow.

Fore wing length 10.4–12.5 mm. Membranes (Fig. 73) faintly yellow, several crossveins margined. Apical band dark brown, separated into a narrow band across apex and several dark brown subapical spots. Pterostigmal band dark brown, broad anteriorly, broken into several dark brown spots posteriorly. Basal band broken into two large spots. First marginal and first basal spots dark brown. Second marginal and second basal spots absent. The wing bands show considerable variation in the size and arrangement of spots. The first marginal spot is usually present, but in several specimens no marginal spots were evident.

Legs dark yellow.

Abdomen dark yellow to reddish yellow. Male terminalia reddish yellow. Ninth tergum (Fig. 103) elongate, emarginate apically, forming two narrow lateral lobes. Hypovalues (Fig. 104) elongate, narrow, tapered posteriorly, ending near bases of dististyles. Dististyles about one-half length of basistyles. Ventral parameres (Fig. 105) elongate, unbranched, barbed, extending well beyond bases of dististyles. Female genital plate (Fig. 146) elongate, 1.61 mm in length. Distal plate short, deeply emarginate apically, forming two narrow lateral lobes. Basal plate oval, elongate. Spermathecal apodeme elongate, widely divergent basally, extending beyond apical emargination of distal plate.

The male terminalia of *P. banksi* closely resemble those of *P. neglecta* although the hypovalues are broader than those of *P. neglecta* and the ventral parameres are barbed.

In Illinois individuals of *P. banksi* were collected in relatively dry areas away from the humid bottomlands. Near Chicago individuals were col-

lected on a dry gravel hillside among wild roses and in narrow steep ravines in cultivated areas.

P. banksi is a northeastern species extending from Georgia to Maine and west to Illinois, Iowa, and Wisconsin.

Illinois Records.—(Fig. 170). Collected from mid-May until early Au-

band dark brown, broken but forked. Basal band reduced to two dark brown spots. Marginal and second basal spots absent. First basal spot dark brown. Considerable variation occurs in the arrangement of the apical and pterostigmal bands.

Legs pale to dark yellow.

Abdomen dark yellow. Male terminalia pale to dark yellow. Ninth tergum, as in Fig. 103, broad basally, apex emarginate, forming two narrow, lateral lobes. Hypovalues (Fig. 106) enlarged medially, tapering apically, ending before bases of dististyles. Dististyles shorter than basistyles. Ventral parameres (Fig. 107) thick, unbranched, with barbs on both margins; parameres sigmoidally curved, extending beyond bases of dististyles, each apex smoothly tapered to acute point. Female genital plate elongate (Fig. 147), 1.39 mm in length, oval. Distal



Fig. 170.—Distribution of *Panorpa banksi* in Illinois and North America.

gust. Restricted to the hilly areas of northern, western, and southern Illinois.

Panorpa sigmoides Carpenter

Panorpa sigmoides Carpenter (1931a: 250). ♂, ♀. Type-locality: Turkey Run [State Park], Indiana.

Head and thorax pale yellow to dark yellowish brown.

Fore wing length 10.7–11.7 mm. Membranes (Fig. 74) clear to pale yellow, crossveins margined. Apical band dark brown, broken into a narrow apical and subapical band. Pterostigmal

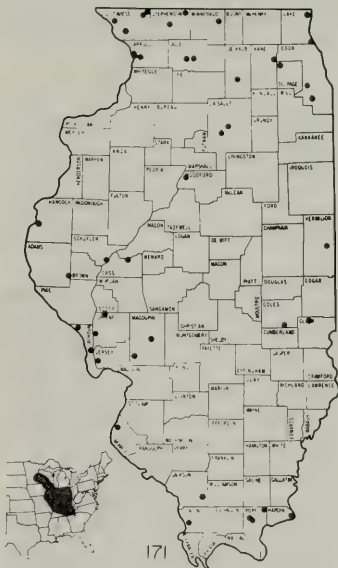


Fig. 171.—Distribution of *Panorpa sigmoides* in Illinois and North America.

plate broad, apex emarginate, forming two narrow lateral lobes. Basal plate broad, oval. Spermathecal apodeme elongate, widely bifurcate basally; apex swollen, extending beyond apical emargination of distal plate. In the female genital plate, significant variation was noted, making the separation of female specimens from *P. banksi* and *P. nebulosa* very subjective.

The male terminalia of *P. sigmoides* resemble those of *P. nebulosa*, but the middle third of the hypovalves is broader in *P. sigmoides*, and the ventral valves are sigmoidally curved.

This species was collected on stinging wood nettle and jewelweed along heavily wooded streams throughout Illinois. It appears to require a moister habitat than most species of *Panorpa*.

P. sigmoides is a midwestern species extending from Tennessee to Ohio and west to Minnesota.

Illinois Records.—(Fig. 171). Collected abundantly from the end of April to early August.

Panorpa nebulosa Westwood

Panorpa nebulosa Westwood (1846: 188). ♀. Type-locality: America boreali. Byers (1962*b*) reported that the female holotype bears the locality Trenton Falls, New York.

Head and thorax dark yellow to dark reddish brown.

Fore wing length 10.2–12.9 mm. Membranes (Fig. 75) clear, crossveins faintly margined. Apical band broken into numerous pale brown spots. Pterostigmal band pale brown, broad anteriorly, forked but broken posteriorly. Basal band reduced to two small brown spots. Marginal and second basal spots absent. First basal spot pale brown.

Legs pale to dark yellow.

Abdomen pale yellow to dark brown. Male terminalia pale yellowish brown. Ninth tergum, as in Fig. 103, broad basally, constricted at apical third, apex emarginate, forming two broad lateral lobes. Hypovalves (Fig. 108) narrow,

elongate, tapered apically, extending three-fourths length of basistyles. Basistyles broad, each with patch of elongate setae at base of dististyle. Dististyles shorter than basistyles. Ventral parameres (Fig. 109) elongate, sinuate, crossing medially, barbed, unbranched, apex narrowed and bare. Female genital plate (Fig. 149) elongate, 1.40 mm in length. Distal plate large, apex emarginate, forming two broad lateral lobes. Basal plate narrowed basally. Spermathecal apodeme elongate, bifurcate basally, apex swollen, reaching slightly beyond apical emargination of distal plate. Considerable variation is evident in the female genital plate, making the separation of *P. nebulosa* from *P. sigmoides* difficult.

The male terminalia of *P. nebulosa* resemble those of *P. sigmoides* although differing in the shape of the ventral parameres. The female of *P. nebulosa* cannot be separated from the *P. acuta* female on the basis of the genital plate.

This species occurs in a wide range of habitats, both wet and dry, always in wooded situations.

P. nebulosa is a wide-ranging eastern species extending from Georgia to Quebec and west to Wisconsin and Missouri (Fig. 172).



Fig. 172.—Distribution of *Panorpa nebulosa* in North America.

Illinois Records.—Collected from early May to late July. DU PAGE COUNTY: Wayne, 19-VII-1947, R. Mit-

chell, 1 ♀. HARDIN COUNTY: Elizabethtown, 22-VI-1932, H. H. Ross, 1 ♂, 1 ♀. LAKE COUNTY: Lake Forest, 6-V-1906, J. G. Needham, 2 ♂. WOODFORD COUNTY: 4 miles W of Cazenovia, 10-VI-1969, Webb and Marlin, 2 ♀. ILLINOIS: Belfrage Collection, Stockholm Museum, 1 ♂, 1 ♀.

Rufescens Group

The *rufescens* group is the largest species-group of *Panorpa*, having 30 species, of which 15 occur in the Midwest. The wing membranes vary from clear to dark yellow and usually have broad apical and pterostigmal bands. The pterostigmal band is generally continuous from the anterior to the posterior margin of the wing. The sixth abdominal tergum of males possesses an anal horn. The ninth tergum of males is emarginate apically, often forming two narrow lateral lobes. The hypovalves (ninth sternum) are fused near the bases of the basistyles.

Panorpa mirabilis Carpenter

Panorpa mirabilis Carpenter (1931a: 229). ♂, ♀. Type-locality: Andover, New Jersey.

Head and thorax dark reddish brown.

Fore wing length 13.3–13.8 mm. Membranes (Fig. 76) clear to pale grey, crossveins not margined. Apical band pale brown, entire, with one or two small clear spots. Pterostigmal band pale brown, continuous, apical fork broken. Basal band pale brown, usually entire, fused with first basal spot along anterior margin. Both marginal and second basal spots absent. First basal spot pale brown.

Legs pale to dark yellow.

Abdomen pale to dark yellow. Male terminalia pale to dark yellow. Ninth tergum, as in Fig. 112, large, broad basally, tapered to shallow apical emargination. Hypovalves (Fig. 111) broad, divergent apically, ending before bases of dististyles. Basistyles narrow, each with small patch of setae near base of dististyle. Dististyles longer than basi-

styles each with large lobe nearly covering dististyle and with pair of large basi-medial lobes. Ventral parameres (Fig. 110) narrow, elongate, unbranched, barbed, extending almost to apices of dististyles. Female genital plate (Fig. 150) large, elongate, 1.58 mm in length. Distal plate deeply emarginate apically. Basal plate absent. Spermathecal apodeme long, extending well beyond base of distal plate but not reaching apical emargination.

The shapes of the hypovalves and dististyles readily associate *P. mirabilis* with *P. galerita*, but the narrow elongate ventral parameres of *P. mirabilis* separate the two species. In females the long spermathecal apodeme and the overall length of the genital plate of *P. mirabilis* readily separate this species from *P. galerita*.

Nothing has been recorded on the habitat of *P. mirabilis*.

P. mirabilis is a northeastern species, recorded from New Jersey, New York, Pennsylvania, and Michigan (Fig. 173).



Fig. 173.—Distribution of *Panorpa mirabilis* in North America.

Panorpa galerita Byers

Panorpa galerita Byers (1962b:472). ♂, ♀. Type-locality: Lake Jean, Ricketts Glen State Park, Sullivan County, Pennsylvania.

Head and thorax pale to reddish yellow.

Fore wing length 12.5–13.7 mm. Membranes (Fig. 77) clear, crossveins not margined. Apical band pale brown,

entire or with few clear spots. Pterostigmal band pale brown, entire, posterior fork usually broken. Basal band pale brown, entire, occasionally fused anteriorly with first basal spot. Marginal and second basal spots absent. First basal spot pale brown.

Legs dark to reddish yellow.

Abdomen reddish brown. Male terminalia reddish brown. Ninth tergum, as in Fig. 112, oval, narrowed apically, apical margin with shallow emargination. Hypovalues (Fig. 113) broad, divergent apically, ending before bases of dististyles. Basistyles broad, each with small medial patch of setae near base of dististyle. Dististyles large, shorter than basistyles, with broad dorsal lobe covering two-thirds of each dististyle and two sinuate basi-medial lobes. Ventral parameres (Fig. 114) thick, sinuate, unbranched, barbed, extending well beyond bases of dististyles. Female genital plate (Fig. 151) short, 0.97 mm in length. Distal plate subtriangular, tapered basally, with concave apical emargination. Basal plate absent. Spermathecal apodeme extending beyond base of distal plate but not reaching apical emargination.

The large lobes of the dististyles, the divergent apices of the hypovalues, and the shape of the ninth tergum readily associate *P. galerita* and *P. mirabilis*. The males of *P. galerita* differ from those of *P. mirabilis* in the thick barbed ventral parameres, the dististyles being shorter than the basistyles, and the

lobes of the dististyles covering only two-thirds of the dististyles. In females the genital plate of *P. galerita* is considerably smaller in length than that of *P. mirabilis*.

Individuals of *P. galerita* have been collected among ferns at the edge of a beech, maple, and hemlock forest.

P. galerita is a northeastern species extending from Quebec and Vermont west to Ohio with a disjunct distribution in Wisconsin (Fig. 174).

Panorpa subfurcata Westwood

Panorpa subfurcata Westwood (1846: 191). ♂, ♀. Type-locality: Nova Scotia.

Panorpa modesta Carpenter (1931a: 233). ♂. Type-locality: Douglas Lake, Michigan. Synonymized by Byers (1974).

Panorpa signifer Banks (1900:251). ♂, ♀. Type-locality: Gaylord, Michigan. Synonymized by Byers (1962b).

Head and thorax reddish to dark reddish brown.

Fore wing length 11.1–14.4 mm. Membranes (Fig. 79) clear, crossveins not margined. Apical band dark brown, broad, with several small clear spots. Pterostigmal band dark brown, broad anteriorly, forked, apical branch may or may not be continuous. Basal band broad, entire. Marginal spots variable. First basal spot dark brown, second basal spot present or absent. Byers (1962b) reported that the marginal spot was absent in all specimens of the type series, as is the case in most of the specimens we examined. However, material examined from Minnesota showed as many as four marginal spots.

Legs reddish to dark reddish brown.

Abdomen reddish brown. Male terminalia reddish brown. Ninth tergum (Fig. 117) long, broad basally, constricted three-fourths way from base; apex emarginate, forming two broad lateral lobes. Hypovalues (Fig. 115) slender, elongate, ending before bases of dististyles. Basistyles broad, each

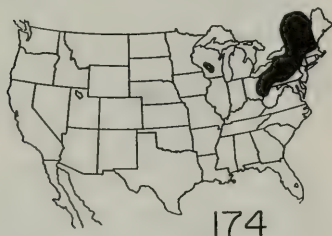


Fig. 174.—Distribution of *Panorpa galerita* in North America.

with patch of elongate setae near base of dististyle. Dististyles large, almost equal in length to basistyles, with large medial lobe. Ventral parameres (Fig. 116) slender, elongate, unbranched, bare, extending well beyond bases of dististyles. Female genital plate (Fig. 153) long, 1.76 mm in length. Distal plate oval, apex emarginate. Basal plate absent. Spermathecal apodeme long, widely divergent basally, not reaching apical emargination of distal plate.

The large lobes of the dististyles relate *P. subfurcata* to *P. mirabilis* and *P. galerita*, but the narrow hypovalves and the elongate, bare ventral parameres readily separate *P. subfurcata* from the latter two species.

Collected in the dense undergrowth of birch-maple woodlands.

P. subfurcata is a northeastern species, extending from North Carolina to Nova Scotia and west to Minnesota and western Ontario (Fig. 175).

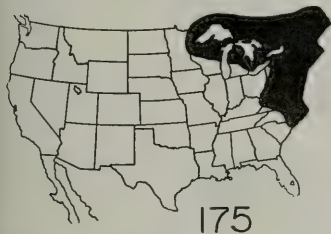


Fig. 175.—Distribution of *Panorpa subfurcata* in North America.

Panorpa hungerfordi Byers

Panorpa hungerfordi Byers (1973a: 367). ♂, ♀. Type-locality: 4 miles west of Pellston, Emmet County, Michigan.

Head and thorax dark reddish brown.

Fore wing length 11.3–12.0 mm. Membranes (Fig. 78) pale yellow, crossveins not margined. Apical band entire, pale brown, with two to four small clear spots. Pterostigmal band pale brown, continuous, forked, with

apical branch broken. Basal band broken into two large pale brown spots. Marginal and second basal spots absent. First basal spot small.

Legs dark yellowish brown.

Abdomen dark reddish brown. Male terminalia reddish brown. Ninth tergum, as in Fig. 117, large, broad basally, tapered to deep apical emargination. Hypovalves (Fig. 118) slender, elongate, extending to base of dististyles. Basistyles broad. Dististyles shorter than basistyles, large, falcate, each with large mesal lobe. Ventral parameres (Fig. 119) slender, unbranched, barbed, extending to middle of dististyles. Female genital plate (Fig. 152) elongate, 0.87 mm in length. Distal plate broad apically, narrowed basally, apex having moderately shallow emargination. Spermathecal apodeme elongate, extending beyond base of distal plate but not reaching apical emargination.

This species was initially identified by authors as *P. virginica*, which it resembles in the shape of the dististyles and the ventral parameres. On closer examination *P. hungerfordi* differs (Byers 1973a) in the absence of a small tooth on each dististyle present in *P. virginica*; these species also differ in the shape of the lobes on the dististyles and in the lengths of the ventral parameres.

Nothing has been reported on the habitat of this species.

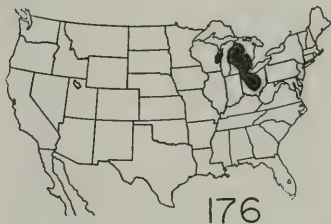


Fig. 176.—Distribution of *Panorpa hungerfordi* in North America.

Panorpa hungerfordi is distributed through Wisconsin, Michigan, and Ohio (Fig. 176).

Panorpa helena Byers

Panorpa helena Byers (1962b:474). ♂, ♀. Type-locality: Swampy woods south of Hopewell Lake, French Creek State Park, Berks County, Pennsylvania.

Panorpa venosa (Authors). Synonymized by Byers (1962b).

Head dark yellow, thorax reddish brown.

Fore wing length 10.9–12.7 mm. Membranes (Fig. 80) clear to amber, crossveins not margined. Apical band dark brown, broad, entire, occasionally having few small clear spots. Pterostigmal band dark brown, broad, apical branch generally separated, forming small spot. Basal band broad, entire. Marginal and second basal spots absent. First basal spot small.

Legs pale yellow, fourth and fifth tarsal segments dark brown to black.

Abdomen dark yellow. Male terminalia dark yellow. Ninth tergum, as in Fig. 117, oblong, rounded basally, tapered apically, deeply emarginate apex forming two broad lateral lobes. Hypo- valves (Fig. 120) moderately thick, extending to bases of dististyles. Basistyles broad, each with one to three dark black setae near bases of dististyles. Dististyles about two-thirds length of basistyles. Ventral parameres (Fig. 121) narrow, elongate, barbed, unbranched, extending to bases of dististyles. Female genital plate (Fig. 154) oval, 1.07 mm in length. Distal plate oval, tapered basally, apex emarginate. Basal plate absent. Spermathecal apodeme elongate, base bifurcate, apex not reaching apical emargination of distal plate.

The dark setae at the bases of the dististyles relate *P. helena* with *P. americana*, but they differ in the shapes of the hypo- valves and the ventral parameres. If the dark setae at the bases

of the dististyles were absent, the male terminalia of *P. helena* would resemble closely those of *P. insolens*.

P. helena is probably the most abundant and widely distributed species of *Panorpa* in North America. It is collected readily in a moist shady woods with a thick herbaceous undergrowth of jewelweed, stinging wood nettle, and poison ivy.

P. helena extends from Georgia to Massachusetts and west to Manitoba, with an isolated record from Utah.



Fig. 177.—Distribution of *Panorpa helena* in Illinois and North America.

Illinois Records.—(Fig. 177). Collected abundantly from early May to mid-October throughout the state.

Panorpa insolens Carpenter

Panorpa insolens Carpenter (1935: 106). ♀. Type-locality: Cincinnati, Ohio.

Head and thorax reddish brown.

Fore wing length 10.9–12.4 mm. Membranes (Fig. 81) pale yellow,

crossveins not margined. Apical band dark brown, entire. Pterostigmal band dark brown to black, entire, broad along anterior margin, forked with apical branch broken. Basal band dark brown, broad, continuous. Marginal and second basal spots absent. First basal spot dark brown, small.

Legs yellowish to reddish brown.

Abdomen reddish brown. Male terminalia dark yellowish brown. Ninth tergum, as in Fig. 117, broad basally, tapering apically to deep emargination forming two thick lateral lobes. Hypovalves (Fig. 126) moderately thick, ending slightly before bases of dististyles. Basistyles broad. Dististyles shorter than basistyles. Ventral parameres (Fig. 127) unbranched, barbed, but bare on apical half, extending to middles of dististyles. Female genital plate (Fig. 157) 0.98 mm in length. Distal plate narrowed basally, wider apically, with deep apical emargination. Basal plate absent. Spermathecal apodeme elongate, extending beyond base of distal plate but not reaching apical emargination.

P. insolens was described by Carpenter on the basis of a single female, which had the basal band of the right fore wing broken at the middle and the upper and lower portions fused with the first basal spot, a condition not present in the left fore wing. The spermathecal apodeme was confined to the distal plate. In the holotype, the broken end of the spermathecal apodeme is evident, and when the portion that was broken off is added to the remainder of the apodeme retained in the distal plate, the apodeme extends beyond the base of the distal plate. We concluded, after comparing the wing patterns and female genital plate of the holotype with specimens collected near the type-locality, that Carpenter based his description on an aberrant specimen. Byers (1973a) has also discussed this variation in Carpenter's holotype of *P. insolens*.

The male terminalia of *P. insolens*

resemble closely those of *P. helena*, though lacking the dark setae near the bases of the dististyles. These species also have differences in the shapes of the ventral parameres.

Collected on stinging wood nettle along shaded streams in northern Kentucky.

P. insolens is known only from southern Ohio and northern Kentucky (Fig. 178).



Fig. 178.—Distribution of *Panorpa insolens* in North America.

Panorpa debilis Westwood

Panorpa debilis Westwood (1846:191).

♀, ♂. Type-locality: America Septentrionali. Byers (1962b) designated the lectotype ♀ and reported the type-locality as Trenton Falls, New York.

Panorpa canadensis Banks (1895:315).

♂. Type-locality: Sherbrooke, Quebec. Synonymized by Byers (1962b).

Head and thorax dark yellow to reddish brown.

Fore wing length 10.4–11.4 mm. Membranes (Fig. 82) colorless, crossveins faintly margined. Apical band dark brown, broad, almost entire except for few pale spots. Pterostigmal band dark brown, apical branch broken, leaving small spot. Basal band brown, separated into two large spots. Marginal and second basal spots absent. First basal spot small.

Legs dark yellow to reddish brown.

Abdomen dark yellow to dark red-

dish brown. Male terminalia reddish brown. Ninth tergum, as in Fig. 117, broad basally, apex deeply emarginate, forming two lateral lobes. Hypovalves (Fig. 128) moderately broad, rounded apically, ending well before bases of basistyles. Basistyles broad, each with cluster of long setae near bases of dististyles. Dististyles shorter than basistyles. Ventral parameres (Fig. 129) elongate, curved, barbed, converging apically, extending beyond bases of dististyles. Female genital plate (Fig. 158) short, 0.79 mm in length. Distal plate narrowed basally, expanded apically, with deep emargination forming two broad lateral lobes. Basal plate absent. Spermathecal apodeme short, not reaching apical emargination of distal plate.

The male terminalia of *P. debilis* resemble those of *P. rufescens*, but the ventral parameres of *P. debilis* converge apically and the hypovalves are broader.

Byers (1954) reported *P. debilis* inhabiting a wide variety of habitats. In southern Illinois it was collected on jewelweed in the Pine Hills area. In central Wisconsin individuals were collected in upland raspberry patches.

P. debilis is an eastern species, extending from North Carolina to Quebec and west to Illinois and Wisconsin, with a doubtful record in Colorado (Fig. 179).



Fig. 179.—Distribution of *Panorpa debilis* in North America.

Illinois Records.—Collected only twice in Illinois in mid-May and early

July. OGLE COUNTY: Grand Detour, 2-VII-1932, Dozier and Mohr, 1 ♂, 1 ♀. UNION COUNTY: Pine Hills, 18-V-1963, W. Brigham, 1 ♂.

Panorpa claripennis Hine

Panorpa claripennis Hine (1901:252).
♂. Type-locality: Sherbrooke, Quebec.

Head and thorax dark reddish brown.

Fore wing length 12.0–14.0 mm. Membranes (Fig. 83) colorless, cross-veins faintly margined. Apical band dark brown, broad, broken posteriorly. Pterostigmal band dark brown, broad anteriorly, tapered posteriorly, with apical branch of fork broken. Basal band broken, forming two large dark brown spots. Marginal and second basal spots absent. First basal spot small.

Legs dark yellow.

Abdomen dark reddish brown. Male terminalia reddish brown. Ninth tergum, as in Fig. 117, elongate, deeply emarginate apically, forming two broad lateral lobes. Hypovalves (Fig. 130) moderately broad, tapered apically, ending before bases of dististyles. Basistyles broad. Dististyles shorter than basistyles. Ventral parameres (Fig. 131) elongate, barbed, extending well beyond bases of dististyles. Female genital plate (Fig. 159) broad, 1.30 mm in length. Distal plate oval, broad, deeply emarginate apically, forming two narrow lateral lobes. Basal plate absent. Spermathecal apodeme broad, bifurcate basally, apex not reaching apical emargination of distal plate.

The male terminalia of *P. claripennis* resemble those of *P. latipennis*, differing in the absence of the basal lobes on the dististyles.

Individuals collected at Otter Creek, Wisconsin, were abundant on jewelweed on a shaded hillside of a steep ravine.

P. claripennis is a northeastern species, extending from Maine and Quebec to Wisconsin with an isolated record from western Florida (Fig. 180).

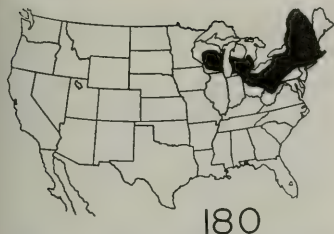


Fig. 180.—Distribution of *Panorpa claripennis* in North America.

Panorpa rufescens Rambur

Panorpa rufescens Rambur (1842:330).
♂, ♀. Type-locality: Amerique septentrionale.

Panorpa venosa Westwood (1846:190).
Type-locality: Georgia. Lectotype ♀ designated by Byers (1962*b*).
Synonymized by Byers (1962*b*).

Panorpa confusa Westwood (1846:190). ♂, ♀. Type-locality: Massachusetts. Lectotype ♂ designated by Byers (1962*b*). Synonymized by Carpenter (1931*a*).

Head and thorax pale to dark yellow.

Fore wing length 11.4–12.4 mm. Membranes (Fig. 84) clear to pale yellow, crossveins not margined. Apical band dark brown, entire, with few clear spots. Pterostigmal band dark brown, entire, posterior fork broken. Basal band broken, forming two large spots. Marginal and first basal spot small. Second basal spot absent.

Legs pale to dark yellow.

Abdomen dark yellow. Male terminalia pale yellow. Ninth tergum, as in Fig. 117, large, broad basally, apex emarginate, forming two broad lateral lobes. Hypovalves (Fig. 122) slender, extending to or just below bases of dististyles. Basistyles broad. Dististyles falcate, with row of coarse setae along mesal margin. Ventral parameres (Fig. 123) slender, barbed, unbranched. Female genital plate (Fig. 155) broad, 0.98 mm in length. Distal plate oblong, broad basally, with apical emargination

forming two broad lateral lobes. Basal plate absent. Spermathecal apodeme extending beyond base of distal plate but not reaching apical emargination.

The male terminalia of *P. rufescens* resemble those of *P. debilis*. However, the hypovalves of *P. rufescens* are narrower and much longer, and the shape of the ventral parameres is different.

Nothing has been reported on the habitat of this species.

Panorpa rufescens is an eastern species extending from Florida to Canada and west to Michigan, Illinois, and Alabama (Fig. 181).



Fig. 181.—Distribution of *Panorpa rufescens* in North America.

Illinois Records.—COOK COUNTY: North Evanston, 20-VIII-1905, W. J. Gerhard, 1 ♀; Bowmanville, 3-VIII-1904, A. B. Wolcott, 1 ♂.

Panorpa dubitans Carpenter

Panorpa dubitans Carpenter (1931*a*: 243). ♂. Type-locality: Hessville, Indiana.

Head and thorax reddish brown.

Fore wing length 9.9–11.8 mm. Membranes (Fig. 85) pale yellow to amber, crossveins margined. Apical band dark brown, broad, with several basal white spots. Pterostigmal band dark brown, broad anteriorly, forked posteriorly, apical fork broken. Basal band broken, forming two dark brown spots. Marginal and first basal spots dark brown. Second basal spot absent. Some variation was noted in the color of the fore

wings and in the size and number of clear spots in the apical band. In 50 percent of the specimens examined, the second marginal spot was absent.

Legs reddish brown.

Abdomen dark yellowish brown to reddish brown. Male terminalia dark yellowish brown. Ninth tergum elongate, base broad, apex emarginate, forming two slender lateral lobes. Hypovalues (Fig. 124) elongate, moderately broad, ending well before bases of dististyles. Basistyles broad, with projection along mesal margin. Dististyles shorter than basistyles. Ventral parameres (Fig. 125) elongate, barbed, unbranched, extending to bases of dististyles. Female genital plate (Fig. 156) short, 0.85 mm in length. Distal plate oval, apex emarginate, forming two broad lateral lobes. Basal plate absent. Spermathecal apodeme elongate, extending well beyond base of distal plate although not reaching apical emargination.

Superficially the male terminalia of *P. dubitans* resemble those of *P. speciosa*, especially in the shapes of the ventral parameres and hypovalues. The males of *P. dubitans* are distinguished from those of *P. speciosa* in having narrower hypovalues, longer basistyles, and fewer and broader barbs, tending to occur in tufts, on the ventral parameres.

In northern Illinois *P. dubitans* was collected on stinging wood nettle along

the bottomlands of Sugar Creek in the Macktown Forest Preserve, Winnebago County.

P. dubitans is a north-central species, occurring in Illinois, Indiana, and Wisconsin (Fig. 182).

Illinois Records.—Collected abundantly from mid-May to early September in northern Illinois. COOK COUNTY: Thornton, 22-VI-1949, Ross and Stannard, 1 ♂; Thornton, Glenwood Forest Preserve, 3-VI-1970, L. J. Stannard, 1 ♂. LAKE COUNTY: Waukegan, 7-VII-1932, T. H. Frison, 1 ♂. WINNEBAGO COUNTY: Macktown Forest Preserve, J. C. Marlin, 16-VII-1969, 1 ♂, 17-VI-1970, 4 ♂, 3 ♀, 4-IX-1971, 1 ♂; D. W. Webb, 10-VII-1970, 2 ♂.

Panorpa speciosa Carpenter

Panorpa speciosa Carpenter (1931a: 243). ♂. Type-locality: Heyworth, Illinois.

Head and thorax pale yellow to dark brown.

Fore wing length 10.7–12.0 mm. Membranes (Fig. 87) clear to amber, crossveins faintly margined. Apical band dark brown, entire, with one or two posterior clear spots. Pterostigmal band dark brown, broad anteriorly, forked, apical fork broken. Basal band broken, forming two large dark brown spots. Marginal and first basal spots small. Second basal spot absent.

Considerable variation was noted in the pattern of the apical and pterostigmal bands. In certain specimens the pterostigmal band is continuous and has both posterior branches. The number of marginal spots varies from one to four. In a few specimens the basal band is weakly continuous.

Legs pale to dark yellow.

Abdomen pale yellow to dark yellowish brown. Male terminalia pale to dark yellow. Ninth tergum, as in Fig. 117, elongate, broad basally, apex emarginate, forming two broad lateral lobes. Hypovalues (Fig. 132) broad, expanded medially, apices rounded, ex-



Fig. 182.—Distribution of *Panorpa dubitans* in North America.

tending three-fourths length of basistyles. Basistyles broad. Dististyles about two-thirds length of basistyles, each dististyle with small patch of elongate setae near base. Ventral parameres (Fig. 133) branched, elongate, barbed, each with apical branch extending slightly beyond base of dististyle. Female genital plate (Fig. 160) short, oval, 1.17 mm in length. Distal plate oval, broad basally, emarginate apically, forming two lateral lobes. Basal plate absent. Spermathecal apodeme elongate, widely bifurcate basally, not reaching apical emargination.

The male terminalia of *P. speciosa* are indistinguishable from those of *P. braueri* although these species can be separated by the characters of the basal band. In the holotype of *P. braueri*, the ventral parameres are very similar to those of *P. speciosa* in being branched, but the mesal branch in *P. braueri* is

somewhat thicker and larger than that in *P. speciosa*. In females the genital plate of *P. speciosa* is much longer than it is in *P. braueri*.

This species has been collected abundantly in Illinois on stinging wood nettle, jewelweed, and poison ivy in humid shaded areas along slow-moving streams.

P. speciosa is a north-central species extending from Arkansas and Tennessee to Minnesota and Wisconsin (Fig. 183).

Illinois Records.—(Fig. 183). Collected frequently from late April until early November. The prolonged collection period indicates the possibility of two generations per year.

Panorpa braueri Carpenter

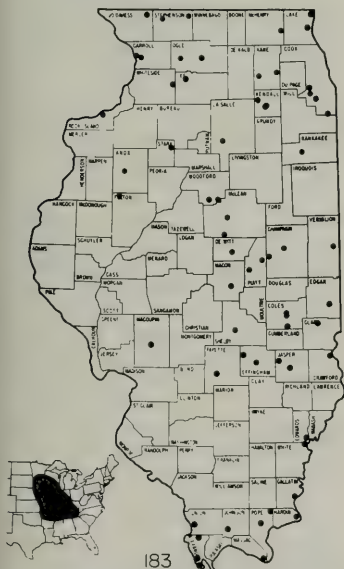
Panorpa braueri Carpenter (1931a: 242). ♂, ♀. Type-locality: Washington County, Arkansas.

Head and thorax dark yellowish brown.

Fore wing length 10.0–11.4 mm. Membranes (Fig. 86) pale yellow, crossveins margined. Apical band dark brown, entire, with several small clear spots. Pterostigmal band dark brown, broad from anterior margin to posterior, apical fork broken, small. Basal band dark brown, broad, continuous. Two marginal spots and first basal spot dark brown. Second basal spot absent.

Legs dark yellowish brown.

Abdomen dark reddish brown. Male terminalia dark yellowish brown. Ninth tergum, as in Fig. 117, elongate, base broad, apex emarginate, forming two broad lateral lobes. Hypovalves (Fig. 134) broad, expanded medially, apices rounded, extending three-fourths length of basistyles. Basistyles broad. Dististyles about two-thirds length of basistyles, each with small patch of elongate setae at base of inner basal cusp. Ventral parameres (Fig. 135) narrow, elongate, each with broad mesal branch and slender apical branch extending beyond base of dististyle. In ventral view the slender apical branch is often



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Fig. 183.—Distribution of *Panorpa speciosa* in Illinois and North America.

hidden, giving the paramere the appearance of having a single, broad, bulbous apex. Female genital plate (Fig. 161) small, broad, 0.69 mm in length. Distal plate broad, deeply emarginate apically, forming two broad lateral lobes. Basal plate absent. Spermathecal apodeme short, not reaching apical emargination of distal plate.

P. braueri is very closely related to *P. speciosa*, and little difference exists in the characters of the male terminalia. These species may be separated by the broad, continuous basal band in the wing of *P. braueri*. In females of *P. braueri* the genital plate is much shorter than that of *P. speciosa*.

Byers (1954) reported collecting Missouri specimens of *P. braueri* on small patches of *Impatiens* in a shaded swale.

P. braueri seems restricted to northwestern Arkansas and southern Missouri (Fig. 184).



Fig. 184.—Distribution of *Panorpa braueri* in North America.

Panorpa bifida Carpenter

Panorpa bifida Carpenter (1935:107).
♂, ♀. Type-locality: Rector, Pennsylvania.

Head and thorax dark yellowish brown.

Fore wing length 12 mm. Membranes (Fig. 88) pale yellow, crossveins not margined. Apical band pale brown, entire, with one or two clear spots. Pterostigmal band pale brown, continuous, apical work broken. Basal band pale brown, broken into two large

spots. Two marginal spots and large first basal spot present. Second basal spot absent.

Legs pale yellow.

Abdomen dark yellowish brown. Male terminalia dark yellowish brown. Ninth tergum elongate, deeply emarginate apically, forming two narrow lateral lobes. Hypovalves (Fig. 136) broad, extending almost to bases of dististyles. Basistyles broad. Dististyles each with small patch of elongate setae near base. Ventral parameres (Fig. 137) narrow, elongate, each with two thin, barbed, branches extending beyond base of dististyle, united basally to form Y-shaped projection. Female genital plate (Fig. 162) broad, 0.99 mm in length. Distal plate broad, deeply emarginate apically to form two broad lateral lobes. Basal plate absent. Spermathecal apodeme elongate, not reaching apical emargination of distal plate.

P. bifida is related to *P. anomala*, but it is easily distinguished from *P. anomala* by the narrow elongate branches of the ventral parameres.

Nothing has been reported on the habitat of this species.

P. bifida is known only from Pennsylvania and Ohio (Fig. 185).



Fig. 185.—Distribution of *Panorpa bifida* in North America.

Panorpa anomala Carpenter

Panorpa anomala Carpenter (1931a: 245). ♂, ♀. Type-locality: Leavenworth County, Kansas.

Panorpa proximata Carpenter (1931a: 247). ♂. Type-locality: Washington

County, Arkansas. Synonymized by Byers (1974).

Head and thorax dark yellow to dark reddish brown.

Fore wing length 10.6–12.4 mm. Membranes (Fig. 89) pale yellow, crossveins faintly margined. Apical band dark brown to black, broad, usually entire. Pterostigmal band dark brown, broad anteriorly, broken posteriorly. Basal band broken, forming two dark brown spots. Two marginal spots and first basal spot small. Second basal spot absent. In most specimens the apical band of the fore wing is broad and entire although several specimens showed the apical band broken into several small dark brown spots and a narrow subapical band. In some specimens a second basal spot was present and the second marginal spot absent.

Legs dark yellow.

Abdomen dark yellow to dark reddish brown. Male terminalia dark reddish brown, oval. Ninth tergum, as in Fig. 117, emarginate apically, forming two broad lateral lobes. Hypovalues (Fig. 140) broad apically, ending well before bases of dististyles. Basistyles broad. Dististyles shorter than basistyles. Ventral parameres (Fig. 141) elongate, barbed, with one branch extending posteriorly beyond bases of dististyles and a mesal branch curved dorsally. Female genital plate (Fig. 163) oval, 1.15 mm in length. Distal plate short, deeply emarginate apically, forming two acute lateral lobes. Basal plate absent. Spermathecal apodeme elongate, bifurcate basally, not reaching apical emargination of distal plate.

The shape of the male terminalia of *P. anomala* resemble somewhat those of *P. elaborata* but differ markedly in the short hypovalues and heavily barbed ventral parameres.

In Illinois *P. anomala* was initially collected along the bottomlands of the Illinois River at Morris in a dense growth of stinging wood nettle. Indi-

viduals in southern Illinois were collected on jewelweed in shaded areas along small creeks.

P. anomala is a western species, occurring from southeastern Tennessee and northwestern Georgia west to Wisconsin, Kansas, and Arkansas (Fig. 186).



Fig. 186.—Distribution of *Panorpa anomala* in Illinois and North America.

Illinois Records.—(Fig. 186). Collected from late May until mid-August in northern, western, and southern Illinois. Carpenter (1931a) erroneously recorded *P. anomala* in Illinois from Starved Rock State Park on the basis of an imperfect female. This specimen has since been identified as a female of *P. speciosa*.

Panorpa consuetudinis Snodgrass

Panorpa consuetudinis Snodgrass (1927:77). ♂. Type-locality: Takoma Park, Maryland. Neotype ♂ designated by Byers (1974).

Panorpa elaborata Carpenter (1931a: 239). ♂, ♀. Type-locality: Falls Church, Virginia. Synonymized by Byers (1974).

Head and thorax dark yellowish brown.

Fore wing length 10.0–11.0 mm. Membranes (Fig. 90) amber, cross-veins margined. Apical band dark brown, broad, with several subapical clear spots. Pterostigmal band dark brown, broad anteriorly, forked posteriorly. Basal band continuous or broken. Marginal and first basal spots small. Second basal spot lacking.

Legs dark yellow.

Abdomen dark yellow. Male terminalia dark yellow. Ninth tergum elongate; base broad, tergum constricted beyond middle, apex deeply emarginate, forming two narrow lateral lobes. Hypovalves (Fig. 138) narrow, elongate, extending to bases of dististyles. Basistyles broad. Dististyles shorter than basistyles. Ventral parameres (Fig. 139) extend beyond bases of dististyles, each paramere with two branches, mesal branch barbed, apical branch with two tufts of barbs. Female genital plate (Fig. 164) short, 0.85 mm in length. Distal plate concave apically, not deeply emarginate, sides parallel.

Basal plate absent. Large, subrectangular, sclerotized membrane covers most of distal plate. Spermathecal apodeme elongate, bifurcate basally, not reaching apical emargination of distal plate.

The male terminalia of *P. consuetudinis* are similar to those of *P. dubitans* although differing in the longer hypovalves and the branched ventral parameres.

Little is known of the specific habitat of *P. consuetudinis*. In Kentucky individuals were collected with specimens of *P. insolens* in densely shaded vegetation along a slow-moving stream.

P. consuetudinis is an eastern species, extending from South Carolina to New York and west to Indiana and Mississippi (Fig. 187).

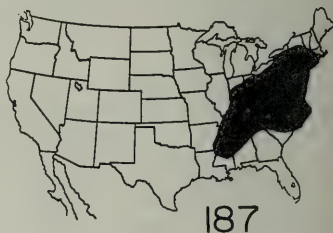


Fig. 187.—Distribution of *Panorpa consuetudinis* in North America.

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**An Electrofishing Survey
of the Illinois River,
1959-1974**

Edward E. Sparks
William C. Starrett

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This report is printed by authority of the State of Illinois, IRS Ch. 127, Par. 58.12. It is a contribution from the Section of Aquatic Biology of the Illinois Natural History Survey.

Richard E. Sparks is an Assistant Aquatic Biologist, and the late William C. Starrett was an Aquatic Biologist, at the Illinois Natural History Survey.

(66938—4M—8-75)



An Electrofishing Survey of the Illinois River, 1959-1974

Richard E. Sparks
William C. Starrett

FROM AS FAR BACK as historical accounts are available, the Illinois River Valley has been described as unusually productive of fish and wildlife. The French explorer Marquette wrote in 1673 (Mills, Starrett, & Bellrose 1966: 3-4):

"We have seen nothing like this river that we enter, as regards to its fertility of soil, its prairies and woods; its cattle, elk, deer, wildcats, bustards, swans, ducks, parroquets, and even beaver."

When Illinois was still a territory, the Illinois River Valley was considered one of the important sources of furs in the northwest part of the United States (Starrett 1972:139). There are older residents of the valley who recall the importance of fish and wildlife to some of the river towns in the early part of the century. Hugh Bell, Superintendent of the Illinois Department of Conservation Fisheries Field Headquarters at Havana, as a young man worked at filling specially constructed tank cars with fish to be shipped by rail from Havana to Chicago. At one time live fish also were shipped regularly to Boston and New York, and the Illinois River ranked as a major inland commercial fishery. There was a U.S. government fisheries station at Meredosia (Forbes & Richardson 1920:XVI). During that same period a train called the Fisherman's Special ran between Springfield and Havana, and there were many people in Havana who made their living outfitting and guiding fishermen and duck hunters.

Because of their importance as unique resources, the Illinois River and its bottomland lakes were studied intensively by the Illinois State Laboratory of Natural History and its succe-

sor, the Natural History Survey, from 1874 to 1927 (Forbes 1928:387). More recently, surveys of the fish populations of the river have been conducted regularly from the 1940's to the present. Various types of sampling gear have been employed in these surveys, for various purposes. For example, minnow seines were used regularly in mid-summer to collect small fish and thereby gauge the spawning success of species which spawn in the spring. Hoop nets were used to collect large fish in backwaters and bottomland lakes. The present report concerns primarily the electrofishing surveys, which have been conducted regularly in the Illinois River in the fall, from 1959 through 1974.

ACKNOWLEDGMENTS

The electrofishing survey of the Illinois River was conceived and carried out, for the most part, by Dr. William C. Starrett, Aquatic Biologist, Havana Field Laboratory, Illinois Natural History Survey. Dennis L. Dooley worked on the electrofishing survey, and other Illinois River studies, for 9 years. Robert Crompton, Howard Crum, and Ron Barker also assisted in the project under Dr. Starrett's direction.

Following Dr. Starrett's death in December, 1971, the electrofishing survey was resumed in 1973 by the writer and Kenneth Walker, with assistance in locating stations and following previously established methods from Mr. Dooley. Carl M. Thompson assisted with the 1974 electrofishing and helped compile and analyze data for this report.

We thank Lloyd LeMere for drawing the figures, Dr. R. Weldon Larimore

for reviewing the manuscript, O. F. Glissendorf for final editing, and Judith L. Breckenridge who did the typing. We are grateful to all the students and other assistants who helped with the program from 1959 through 1974.

Finally, the electrofishing survey could not have been continued in 1974 without the support of the St. Louis District and the Waterways Experiment Station of the U.S. Army Corps of Engineers.

PROCEDURE

Twenty-four sampling sites were chosen in 1959 that provided good habitat for adult fish and that were fairly well distributed throughout the length of the river (Table 1). The same sites were usually sampled in succeeding years, except that one additional station, Big Blue Island Chute, was sampled in 1974. Most of the sites are in chutes, that is, side channels of the river, and contain brush piles, undercut banks, and "holes" where various species of fish are apt to congregate. The four exceptions to this general description are (1) the station above Pekin where both sides of the main channel were fished, (2) the station along the shore of Lower Peoria Lake, (3) the station in Middle Peoria Lake where docks and riprapping in various marinas were fished in the 1960's and where riprapping at a state conservation landing in Detweiller Park was fished in the 1970's, and (4) a station in the Des Plaines River where the wide mouth of the Du Page River and a boatyard were fished. The stations are located most accurately by river mile*—the exact number of miles upstream from the mouth of the river at Grafton, based on the Corps of Engineers' chart book of the Illinois Waterway (U.S. Army Engineer District, Chicago 1970). A river mile designation shows the approximate area that was fished. For example, at the

first station listed in Table 1, we fished that part of Mortland Island Chute which extended from mile 18.7 to mile 19.4.

Pools in Table 1 refer to the waters impounded behind the dams and locks for navigation. Throughout this paper, references are made to these pools as convenient geographic locations of the various sections of the river. The lower part of the Illinois River is under the influence of the Alton Dam on the Mississippi. The dams forming the other pools, in upstream order, are: La Grange (river mile 80.2), Peoria (mile 157.6), Starved Rock (mile 231.0), Marseilles (mile 247.0), and Dresden (mile 271.5). Because the upstream pools are shorter than the downstream ones, there are fewer stations in the upstream pools.

The Illinois River begins at the confluence of the Des Plaines and Kankakee Rivers, and a distance of only 1.4 miles (2.25 km) separates the confluence and Dresden Dam. The Dresden Pool extends into the Des Plaines and Kankakee Rivers, and our one sampling station in the Dresden Pool is actually located in the Des Plaines River. The Kankakee is a relatively unpolluted stream, while the Des Plaines River receives municipal and industrial effluents from the Chicago metropolitan area, via the Chicago Sanitary and Ship Canal. The Des Plaines station is excluded when results from the Illinois River stations are used to compute average yearly catches per unit effort for the whole Illinois River (Tables 3-27).

The navigation dams help to maintain a 2.74-m deep navigation channel by impounding water during low-flow periods. When the water is thus impounded the river behind the dam is said to be at pool stage. In order to sample under similar environmental conditions from year to year, electrofishing was conducted at the same time every year, from late August to the middle of October, and only when the river was in pool behind each of the navigation dams. Not all stations could

* Stations are located by river miles rather than by kilometers because existing river charts and navigation aids along the river use mileages.

be fished every year, because of high water levels, and no stations were fished in 1971 and 1972 due to high water. In addition, the Des Plaines River station was fished only in 1959, 1962, 1973, and 1974, because it is not part of the Illinois River proper and was omitted whenever there was a limited amount of time available for sampling.

Several physical-chemical measurements were made at each station before sampling of the fish populations began. Dissolved oxygen concentrations at a depth of .91 m and at the bottom in the deepest part of the station were measured by the Winkler azide method and, in 1974, with a YSI Model 57 dissolved oxygen meter. Surface water and air temperatures were measured with a mercury thermometer. Wind direction and velocity and cloud cover were noted. Transparency was measured with a Secchi disk. In addition, turbidity of the river was measured with a Jackson turbidimeter during some surveys.

Fish populations were sampled by means of electrofishing. Fish were stunned by an electric current produced by a 230-volt, 180 cycles/sec, AC generator (Homelite 9HY-1), and transmitted through the water via three cables suspended from booms in the front of a 5.49-m aluminum boat. The stunned fish were dipped from the water and placed in plastic garbage cans containing water. Electrofishing was conducted in 15-minute segments, and a total of 60 minutes was spent electrofishing at most stations. In small chutes, or where an abundance of fish was collected quickly, only 30 minutes were spent electrofishing. Fish were identified, counted, weighed, checked for disease, and returned to the river. The few fish that died were buried on shore.

RESULTS

PHYSICAL-CHEMICAL RESULTS

Physical-chemical results for the fall of 1974 are shown in Table 2. Since

the dissolved oxygen levels at both the .91-m depth and on the bottom were approximately the same at every station, the water was presumably well mixed. The dissolved oxygen concentration was 77-97 percent of saturation in the Alton Pool, 65-122 percent of saturation in La Grange and Peoria Pools, and 47-104 percent of saturation in Starved Rock, Marseilles, and Dresden Pools. At Ballard Island Chute (mile 247.8-248.2) and in Lower Peoria Lake (mile 163.0-163.4), the atypically high oxygen values (greater than saturation) were probably due to algal photosynthesis, since the waters had a greenish or brownish tinge. Ballard Island Chute is shallow, and has a large surface area, slow current, and a very dissected shoreline, with many marshy blind pockets. Thus, it should be a likely spot for phytoplankton to develop. The Secchi disk visibility here was much lower than in the river, although some of the turbidity on the sampling date can be attributed to wave action on the shallow bottom, as well as to phytoplankton.

The upper river in 1974 was generally more transparent, as measured by the Secchi disk, than the lower river. Starrett (1971:273) found that turbidity readings with a Jackson turbidimeter were higher in the lower three pools than in the upper three pools in the period 1963-1966. The Alton, La Grange, and Peoria Pools are generally more turbid than the upper pools, presumably because the lower pools have soft mud bottoms and receive heavy silt loads from tributary streams that drain agricultural areas. The river above Hennepin (mile 207.5) generally has a rocky bottom, although the rock is overlaid with mud, sand, and/or gravel in some sections.

Towboats (several barges pushed by a diesel-powered boat) have a marked effect on turbidity in the Illinois River. Fig. 1 shows that the turbidity in mid-channel at mile 25.9 was increased by about 100 Jackson turbidimeter units (JTU) as towboats passed on three

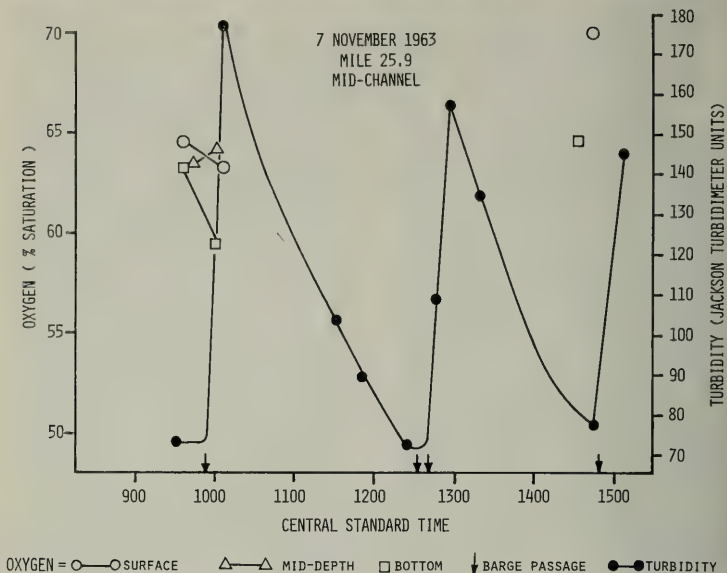


Fig. 1.—Dissolved oxygen concentrations and turbidity in the middle of the navigation channel of the Illinois River at mile 25.9, during passages of towboats on 7 November, 1963. Symbols for dissolved oxygen are circles for at the surface, triangles for at mid-depth, and squares for at the bottom. Turbidity is indicated with black dots. The time at which each towboat passed mile 25.9 is marked by an arrow.

occasions on 7 November, 1963. It took approximately 2½ hours for the turbidity to return to background levels following passage of towboats.

A Natural History Survey crew took a few dissolved oxygen readings in midchannel on 6 and 7 November, 1963, before, during, and after towboats had passed (Fig. 1 and 2). One might expect turbulence from movement of the hulls and from the propellers to aerate the water. Surprisingly, oxygen levels at the surface declined and then recovered following passage of a towboat on 6 November. On 7 November, oxygen levels at both the surface and bottom declined. The declines are significant; oxygen levels at the surface on 6 November and at the bottom on 7 November declined by 0.4 mg/l, and the standard deviation

of the method used (azide modification of the Winkler method) is 0.1 mg/l, even in the presence of appreciable interference. The decline in dissolved oxygen and the increase in turbidity are both attributable to the resuspension of sediment caused by towboats moving in the relatively shallow navigation channel (2.74 m deep). Sediments in the Illinois River exert an appreciable oxygen demand, and the demand increases 7-fold to 10-fold when the sediments are disturbed. For example, Butts (1974:12) reported an oxygen demand of 2.8 g/m²/day for sediment at mile 198.8, under quiescent conditions, and 20.7 g/m²/day when the sediments were disturbed. The disturbance was produced by water current within a special chamber which Butts had constructed to measure in

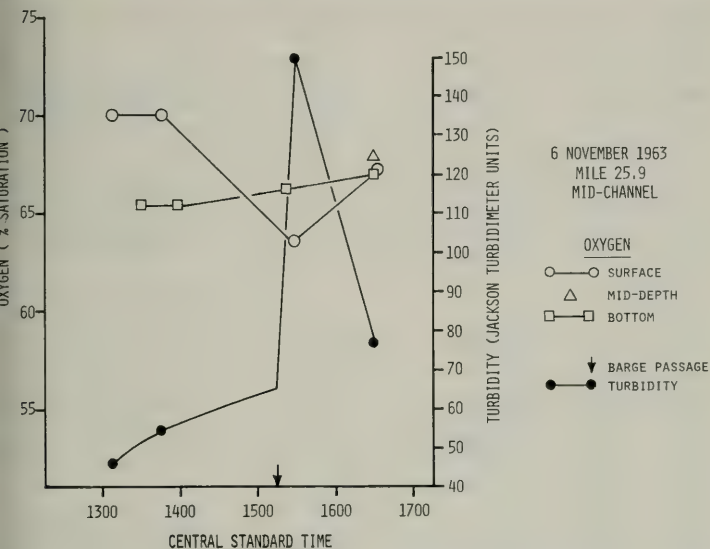


Fig. 2.—The effects of towboat passage on dissolved oxygen concentrations and turbidity at the same location on 6 November, 1963. The symbols are the same as in Fig. 1.

in situ oxygen demand, and could logically be equated to the effects of disturbances created by barges (Butts 1974:6).

It is not known why oxygen levels increased slightly at the bottom on 6 November, and at mid-depth on 7 November, following passage of towboats. It may be that turbulence from towboats results in uneven mixing of parcels of water aerated by turbulence with parcels of water deoxygenated by resuspended sediment.

The water temperatures in Starved Rock, Marseilles, and Dresden Pools were generally higher than in the upper part of Peoria Pool, even though the readings in the upper pools were taken 2 weeks later and the weather had turned colder. The upper river is evidently warmer because of warm industrial and municipal discharges. Starrett (1971:370–373) reported the same

trend of warmer temperatures in the upper river in July and August, 1966.

ELECTROFISHING RESULTS

The electrofishing results for those species that were frequently taken are presented below in phylogenetic order.

Shortnose Gar (Table 3)

Table 3 shows that shortnose gar (*Lepisosteus platostomus*) were occasionally taken in the three downstream pools, but never taken in the three upstream pools. Judging by the reports of commercial fishermen, shortnose gar are more abundant in the downstream pools than our records indicate, and these fish are probably less vulnerable to electric shock than other species. Although garfish are listed in the commercial catch from the Illinois River (Table 28) most fishermen consider them a nuisance because they easily become entangled in nets, with their

elongate snout and numerous sharp teeth, and there is little demand for them as a food fish.

Bowfin (Table 4)

Bowfin (*Amia calva*) is considered a commercial species, but was not common in the Illinois River collections. Bowfin were taken as far upstream as Peoria Pool only in 1961, and otherwise were restricted to collections from La Grange and Alton Pools. Bowfin taken from Alton Pool in 1974 were in breeding color.

Gizzard Shad (Table 5)

Gizzard shad (*Dorosoma cepedianum*) were most abundant in La Grange and Peoria Pools and were generally abundant in our collections in all pools of the river. The numbers and pounds reported in Table 5 do not begin to reflect the actual abundance of the species, for two reasons. One is that small gizzard shad are stunned only momentarily by the electric shock, and usually get away before they can be netted. The second is that so many gizzard shad usually appear that it is futile to try to net them all, and our netting efforts are concentrated on the other species.

Gizzard shad are neither a commercial nor a game species, but small shad are valuable forage for largemouth bass, crappies, and even species such as drum, which ordinarily prefer molluscs when they are available.

Shad are sensitive to low oxygen and probably sensitive to cold temperatures, and die-offs of gizzard shad sometimes occur in the bottomland lakes and backwaters in midsummer and usually occur in winter. Nevertheless, because of their high reproductive capacity, gizzard shad populations do not seem to be much affected by these die-offs.

Goldeye, Mooneye (Tables 6 and 7 — Discussed under "Species Infrequently Taken")

Goldfish, Carp x Goldfish Hybrids (Tables 8 and 9)

Goldfish (*Carassius auratus*) were probably introduced into the Illinois River between 1908 and 1935; Forbes & Richardson do not mention them in *The Fishes of Illinois* (1920) and O'Donnell (1935) mentions that they occur frequently in the Illinois River. O'Donnell (1935) also mentions that two carp x goldfish hybrids were taken at Peoria.

Goldfish and carp x goldfish hybrids were generally abundant in the Des Plaines and upper Illinois electrofishing collections from 1959 through 1974 (Fig. 3 and 4). Goldfish were usually most abundant in Dresden, Marseilles, and Starved Rock Pools, and carp x goldfish were most abundant in Peoria and Starved Rock Pools from 1964 through 1974.

The catch of goldfish generally declined in the downstream direction. From 1959 through 1974 no goldfish were taken in the Alton Pool, although carp x goldfish hybrids were taken from the Alton Pool in 1974 for the first time. Following the period of high water, 1971–1973, the number of goldfish taken from the whole river in 1973 and 1974 declined dramatically. The carp x goldfish hybrids did not exhibit such a dramatic decline. Hybrids may occur in the polluted upper river because "hybrid vigor" confers some resistance to pollution, or simply because both carp and goldfish occur there.

Carp (Table 10)

Carp (*Cyprinus carpio*) were introduced into the Illinois River in 1885. By 1898, carp brought more money to commercial fishermen along the Illinois River than all other fishes combined. The carp catch was 6–8 million pounds (2,720,000–3,630,000 kg) per year and was worth more than \$200,000 (Forbes & Richardson 1920:105–106). In 1908 the catch was over 15 million pounds (6,800,000 kg), according to Thompson

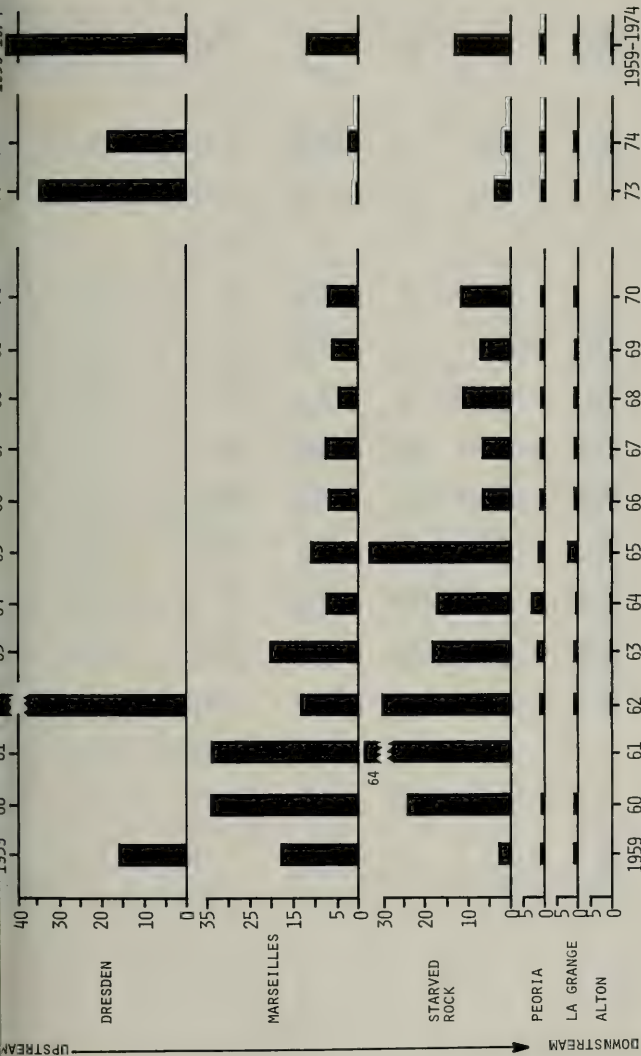


Fig. 3.—The number of goldfish taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959–1974 are shown in the last column. When electrofishing was conducted, but no fish were taken, a very small bar is shown on the figure. Where no electrofishing was conducted, there is no bar. To determine whether a small number of fish or no fish were taken, refer to the text or the tables.

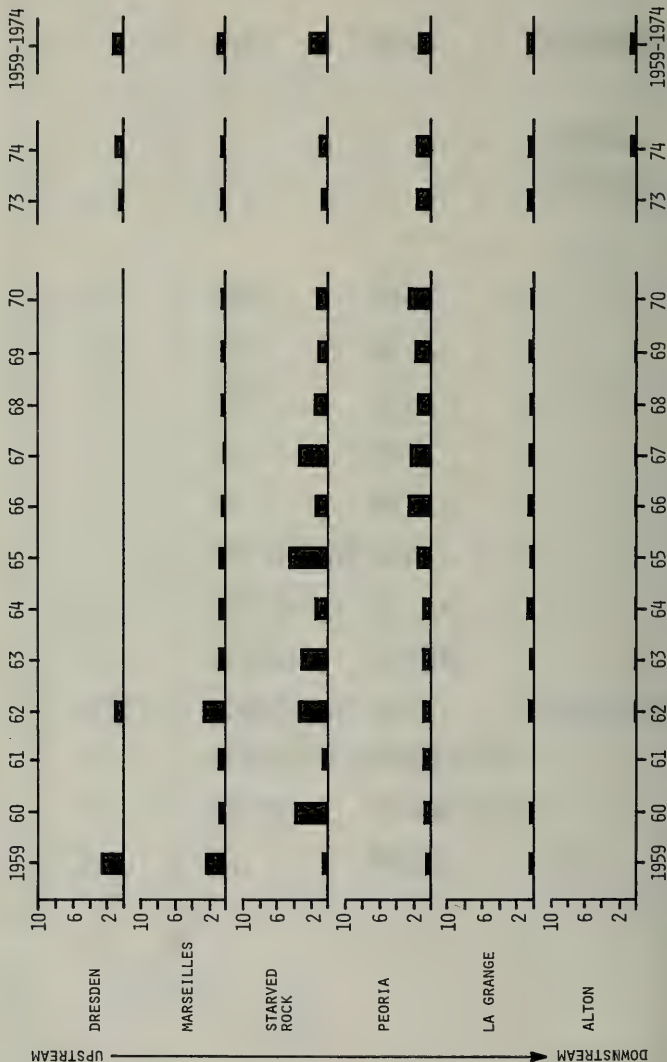


Fig. 4.—The number of carp x goldfish hybrids taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959-1974 are shown in the last column. When electrofishing was conducted, but no fish were taken, a very small bar is shown on the figure. Where no electrofishing was conducted, there is no bar. To determine whether a small number of fish

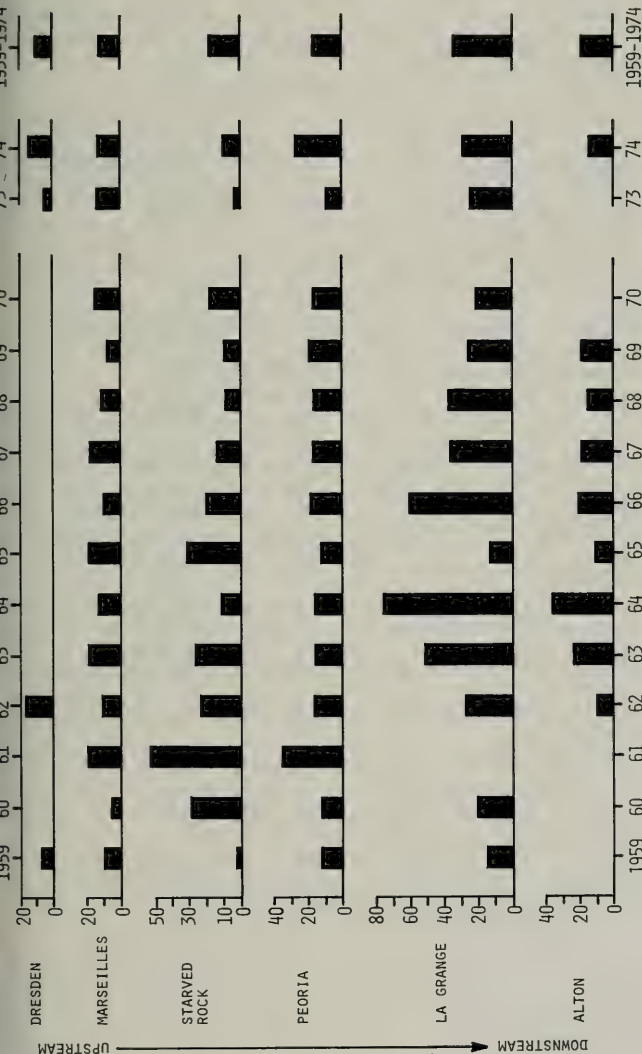


Fig. 5.—The number of carp taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959-1974 are shown in the last column. (Gizzard shad, like carp, were abundant throughout the river.) When electrofishing was conducted, but no fish were taken, a very small bar is shown on the figure. Where no electrofishing was conducted, there is no bar. To determine whether a small number of fish or no fish were taken, refer to the text or the tables.

(1928:285). At present, carp and gizzard shad are the only species that occur abundantly in our electrofishing collections in all pools of the river (Fig. 5). Carp and bigmouth buffalo comprise the bulk of the commercial catch in the Illinois River. The carp catch from the Illinois River was 213,000 pounds (104,000 kg) in 1973.

River Carpsucker, Quillback

Carpsucker (Tables 11 and 12)

The greatest number of quillback carpsuckers (*Carpiodes cyprinus*) was usually taken in three pools of the Illinois River: Marseilles, Starved Rock, and Peoria.

In contrast to the quillback, the most river carpsuckers (*Carpiodes carpio*) were generally taken in the three lower pools, Alton, La Grange, and Peoria, prior to 1973. In 1973 and 1974 most were taken in Starved Rock Pool, so their distribution in the river may have changed after the high-water period 1971–1973. The quillback and river carpsuckers are both commercial species.

Smallmouth Buffalo (Table 13)

The largest numbers of smallmouth buffalo (*Ictiobus bubalus*) were taken from Peoria and La Grange Pools. An unusually large number of smallmouth buffalo were taken from Starved Rock Pool in 1974. The smallmouth buffalo is a commercial species.

Bigmouth Buffalo (Table 14)

Like the smallmouth buffalo, the bigmouth buffalo (*Ictiobus cyprinellus*), was most commonly taken in Peoria and La Grange Pools. Prior to 1974 no bigmouth buffalo had been taken from Dresden and Marseilles Pools, and bigmouth buffalo had been taken in Starved Rock Pool in only one year, 1966. In 1974 they were taken in both Starved Rock and Marseilles Pools. It is surprising that few buffalo were ever taken in Alton Pool, and that no buffalo were taken there in 1974. Several commercial fishermen at Kampsville Landing and Godar Landing on

the Alton Pool said that they also were catching very few bigmouth buffalo in 1974. Bigmouth buffalo rank second to carp in the commercial catch from the Illinois River.

Black Buffalo (Table 15)

The black buffalo (*Ictiobus niger*) is a commercial species. It was not abundant in the Illinois River electrofishing collections, and was taken only in the lower three pools prior to 1974. It was most commonly taken in Peoria and La Grange Pools. In 1974, the few black buffalo taken all came from Starved Rock Pool.

Shorthead Redhorse (Table 16 — Discussed under "Species Infrequently Taken")

Black Bullhead (Table 17)

The black bullhead (*Ictalurus melas*) is considered a commercial species, but most of the bullheads in our electrofishing collections were quite small.

Most of the black bullheads were taken from one station, Ballard Island Chute (river mile 247.8–248.2) in Marseilles Pool (Fig. 6), which was described earlier as being an unusually shallow, broad, marsh-fringed area, with very little current. The black bullhead probably prefers this type of habitat.

Black bullheads were collected occasionally in the main navigation channel, by means of an otter trawl. For example, on 26 August, 1964, 51 black bullheads averaging 18 cm in total length were taken in 49 minutes of trawling at mile 193.

Yellow Bullhead (Table 18 — Discussed under "Species Infrequently Taken")

Channel Catfish (Table 19)

Channel catfish (*Ictalurus punctatus*) were taken in Marseilles Pool for the first time in 1974. Also, the second largest number and weight of fish were taken in the river in 1974 (Fig. 7). Most channel catfish were taken below Beardstown (river mile

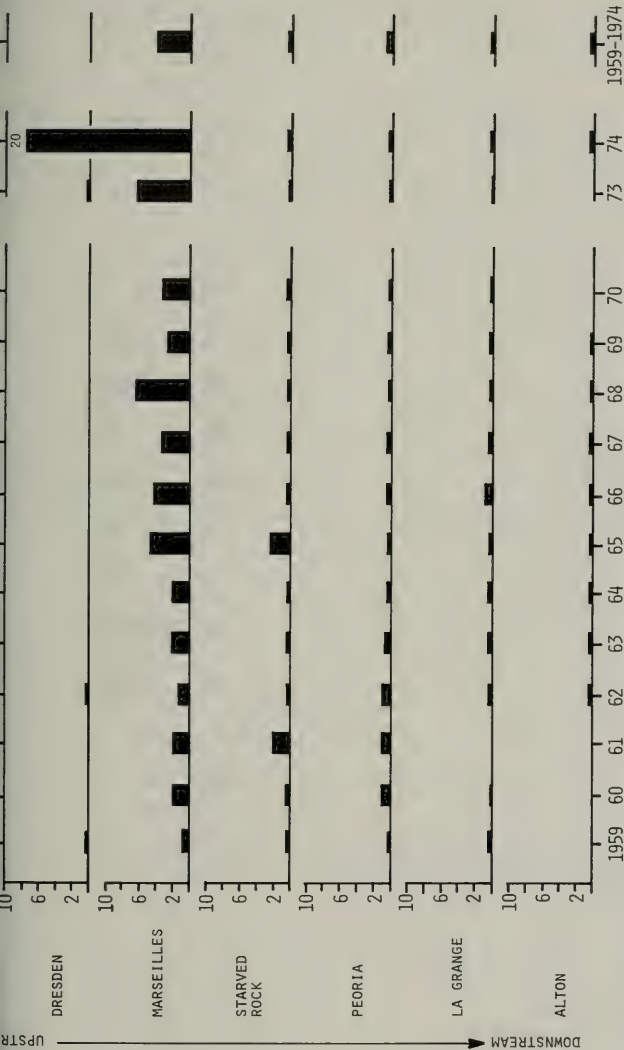


Fig. 6.—The number of black bullheads taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959-1974 are shown in the last column. (The black bullhead was the only species restricted primarily to one station within one pool.) When electrofishing was conducted, but no fish were taken, a very small bar is shown on the figure. Where no electrofishing was conducted, there is no bar. To determine whether a small number of fish or no fish were taken, refer to the text or the tables.

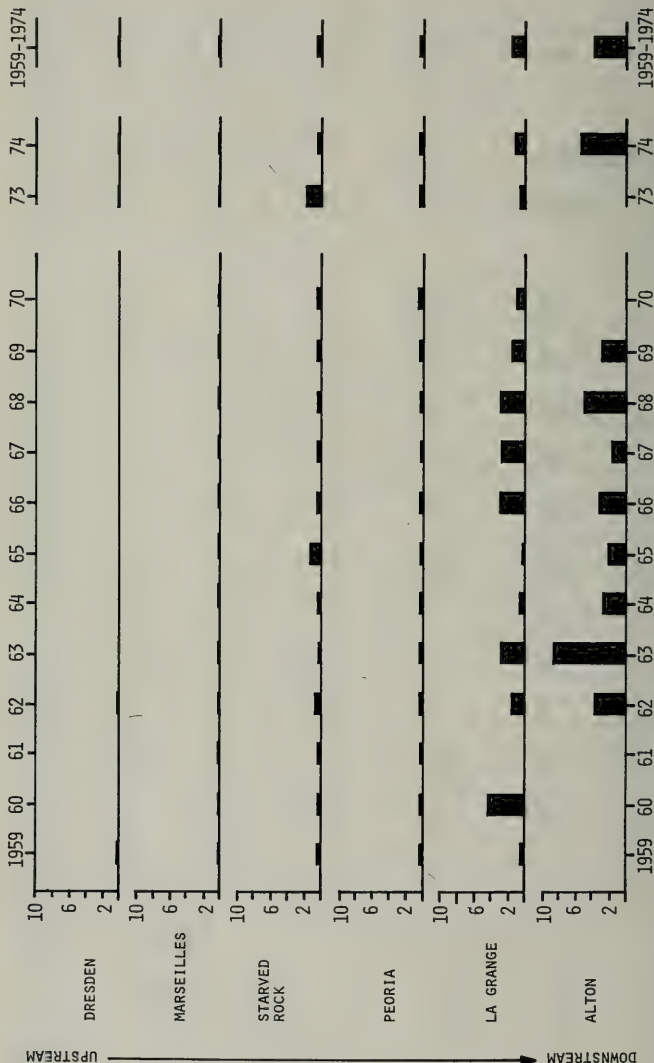


Fig. 7.—The number of channel catfish taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959-1974 are shown in the last column. (Shortnose gar, bowfin, goldeye, mooneye, flathead catfish and white bass showed a similar pattern of increasing numbers in the downstream direction, toward the Mississippi River.) When electrofishing was conducted, but no fish were taken, a very small bar is shown on the figure. Where no electrofishing was conducted, there is no bar. To determine whether a small number of fish or no fish were taken, refer to the text or the tables.

88.5). They were taken occasionally from the main navigation channel by trawling. On 13 November, 1964, 68 young channel catfish averaging 9 cm in total length were taken in 53 minutes of trawling in the channel at mile 156. Prior to 1973, the numbers and weights of channel catfish taken appear to be unrelated to water levels. Channel catfish have declined in the Illinois River since 1899 as evidenced by the following commercial fishing statistics: 241,000 pounds (109,316 kg) in 1899, 105,554 pounds (47,878 kg) in 1950, about 98,000 pounds (44,452 kg) in 1964 (Mills, Starrett, & Bellrose 1966:17), and 45,000 pounds (20,412 kg) in 1973. (Larry Dunham, Fishery Biologist, Illinois State Department of Conservation, personal communication.)

Flathead Catfish (Table 20)

Flathead catfish (*Pylodictis olivaris*) are a desirable commercial species and often reach weights of 9–18 kg. Flathead catfish were never abundant in the electrofishing collections, and were confined to the lower two pools. An 8.16-kg individual was taken in La Grange Pool and several 1- or 2-year-old flatheads were taken at several stations in both Alton and La Grange Pools in 1974.

White Bass (Table 21)

The white bass (*Morone chrysops*) is a game species. The largest number of white bass was taken from the river in 1974, but the greatest catch by weight was in 1968. White bass populations generally increased in the downstream direction, with the largest number and greatest weights usually taken in Alton Pool.

Green Sunfish (Table 22)

Green sunfish (*Lepomis cyanellus*) are considered game fish by some people, although they do not grow as large as their relative, the bluegill. The green sunfish was taken in the Des Plaines River in two of the four years this station was sampled, whereas the bluegill was never taken from this sta-

tion. The largest numbers of green sunfish were generally taken in Peoria Pool. The number of green sunfish taken did not increase dramatically after the high-water period 1971–1973, as did the number of bluegills.

Bluegill (Table 23)

The largest number and greatest weight of bluegills (*Lepomis macrochirus*) per 30 minutes of electrofishing were taken in 1974. Bluegill populations generally increase in the downstream direction, with either Alton or La Grange Pools having the greatest number and weight. However, in only one year, 1969, were more bluegills obtained in Starved Rock Pool than in the next pool upstream.

Largemouth Bass (Table 24)

The largemouth bass (*Micropterus salmoides*) is a game species. Largemouth populations generally increase in the river in a downstream direction (Fig. 8), with the greatest numbers taken from La Grange and Peoria Pools. However, fewer bass were taken at the two stations in Starved Rock Pool than at the three stations in the next pool upstream, Marseilles. Bass populations in the river as a whole reached their peak in 1960 and 1961, then showed a drastic decline during and following the drought years 1962–1964. The recent increase in largemouth populations follows the high-water years 1971–1973.

Crappies (Tables 25 and 26)

The largest catch of both black crappie (*Pomoxis nigromaculatus*) and white crappie (*Pomoxis annularis*), in weight and numbers, was taken in the river in 1974, following the high-water years 1971–1973. Populations of both species showed a steady decline in the years 1962–1965, during a drought period. Prior to 1973, few crappies were taken in the upper three navigation pools, but increased numbers of both species were taken in the Starved Rock and Marseilles Pools in 1974. In 1962,

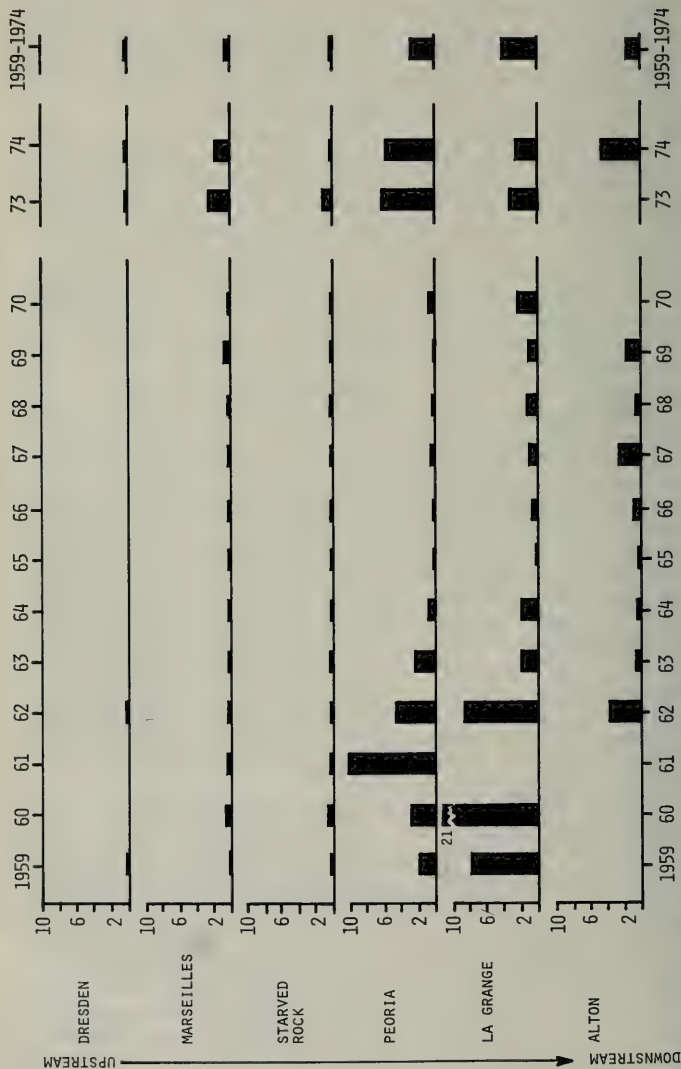


Fig. 8.—The number of largemouth bass taken per 30 minutes of electrofishing in the Illinois River, arranged by pool and year. The average numbers taken during the years 1959-1974 are shown in the last column. (The following species were also most abundant in collections from Peoria and La Grange Pools: gizzard shad, carp, river carpsucker, smallmouth buffalo, black buffalo, yellow bullhead, green sunfish, bluegill, white crappie, black crappie, and freshwater drum.) When electrofishing was conducted, but no fish were taken, a very small bar is shown on the chart.

1964, 1966-1969, and 1974, more black crappie were taken in La Grange Pool than in Alton Pool, perhaps because more backwater and side channel areas with brush piles (a favorite habitat of crappie) were usually available in La Grange Pool. In 1974 a larger number of small white crappie was taken in La Grange Pool than in Alton Pool but a greater weight of large white crappie was taken in Alton Pool. Both species are popular game fish.

Freshwater Drum (Table 27)

Freshwater drum (*Aplodinotus grunniens*) is a commercial species. Most were taken in La Grange Pool. The largest number of individuals and the second greatest weight were taken in 1974, following a high-water period.

Species Infrequently Taken

The yellow bullhead (*Ictalurus natalis*) (Table 18) was uncommon in our collections, and has been taken only from the three lower pools, Alton, La Grange, and Peoria.

The shorthead redhorse (*Moxostoma macrolepidotum*) (Table 16) occurred sporadically in our collections throughout the river.

A female spotted gar (*Lepisosteus oculatus*) was taken by a commercial fisherman at Havana on 26 February, 1973. Spotted gar are uncommon in the Illinois River. This specimen was the largest that had been taken in Illinois (3.41 kg, 83.8 cm in total length) and was full of ripe eggs.

Mooneye (*Hiodon tergisus*) (Table 7) were taken rarely, and only from the Alton Pool until 1974, when one was taken from upper Peoria Pool at mile 215. Goldeye (*Hiodon alosoides*) (Table 6) were taken rarely, but ranged farther upstream than their relative, the mooneye. In 1974 only two goldeye were taken, both from one station at mile 261 in Marseilles Pool.

The American eel (*Anguilla rostrata*) was rarely taken. One was taken from

Alton Pool at mile 19 and two from Peoria Lake in 1974.

The white catfish (*Ictalurus catus*) is a native of brackish to fresh waters along the East Coast from Pennsylvania to Florida. It has been introduced widely in the Midwest, and several have been taken from the Illinois River by commercial fishermen at Havana, including one on 13 May, 1974. White catfish have never been taken in our electrofishing surveys.

The few smallmouth bass (*Micropterus dolomieu*) that were taken were probably introduced from tributary streams that are smaller and colder than the Illinois River.

Skipjack herring (*Alosa chrysochloris*) were taken sporadically throughout the Illinois River. Large numbers apparently moved up the river during the spring flood of 1973, and sport fishermen were catching them on minnows at Havana.

One sauger (*Stizostedion canadense*) was taken at Big Blue Island Chute (river mile 57.5-58.9) in 1974. This species was common in the river before 1908 (Forbes & Richardson 1920:275).

Orange-spotted sunfish (*Lepomis humilis*) and pumpkinseeds (*Lepomis gibbosus*) were taken sporadically.

One species, the longear sunfish (*Lepomis megalotis*), listed as being extirpated from the Illinois River and its bottomland lakes between 1908 and 1970, by W. C. Starrett and P. W. Smith (Starrett 1972:163), was taken from La Grange Pool, Turkey Island Chute (mile 147.3-148.2) on 5 September, 1973. Three adults, ranging in total length from 10.7 to 15.5 cm were taken.

Northern pike (*Esox lucius*) were taken by sport fishermen in the river below Marseilles Dam in 1973, and were netted in Lake Chautauqua in 1973 (river mile 126.0), but were not taken by electrofishing. Northern pike were common in the river before 1908 (Forbes & Richardson 1920:209).

Catfishes may be more abundant in the river than our collections indicate. They are bottom-dwelling species and when shocked they do not always come to the surface where they can be seen to be netted. Under nearly ideal conditions for electrofishing, Larimore (1961) reported taking only 10 percent of the total population of catfishes in a reach of Jordan Creek, whereas 52 percent of the sunfishes were taken. In the generally turbid waters of the lower Illinois River, a fish must be within 10–15 cm of the surface to be seen. So our collecting efficiency for catfishes must have been lower than the 10 percent obtained by Larimore in clear water.

Since we used a shocker, and 6.35 mm mesh dip nets, minnows and other small fishes were generally not taken. We did obtain emerald shiners (*Notropis atherinoides*) throughout the river in 1974 and in previous years (Mills, Starrett, & Bellrose 1966:15).

DISCUSSION

HISTORICAL CHANGES IN THE FISH POPULATIONS OF THE ILLINOIS RIVER

The Illinois-Michigan Canal along the upper Illinois River was completed in 1848, before any biological data were being collected on the Illinois River. Prior to 1871, it is unlikely that this canal had much of an impact on the middle and lower sections of the river, below Hennepin (river mile 208), which are the sections most productive of fish and wildlife. These are the most productive because the Illinois River below Hennepin follows a large valley developed in the late Pleistocene epoch, and the Illinois has developed lateral levee lakes, side channels, backwaters, and marshes which fill this ancient valley and provide excellent habitat for fish and wildlife.

In 1871, the flow of the Chicago River was reversed in order to conduct sanitary wastes from the city of Chicago away from Lake Michigan, which

served as the drinking water supply for the city. The polluted waters of the Chicago River were directed through the Illinois-Michigan Canal into the Des Plaines River and thence into the Illinois River. Some of the polluted water apparently backed up into the lower reaches of the Kankakee. The effect of the polluted water on the fishes of the Kankakee and Illinois rivers was dramatic, according to a report by Nelson (1878:798):

"Previously to the opening of the Chicago River into the canal in 1871, rock-bass, (*Ambloplites rupestris*); black-bass, (*Micropterus pallidus*); largemouth bass, (*Micropterus salmoides*); silver bass, (*Roccus chrysops*) [white bass, *Morone chrysops*]; wall-eyed pike, (*Stizostedion vitreum*) [walleye, *Stizostedion vitreum*]; mud-pike, (?); pickerel, (*Esox lucius*) [northern pike, *Esox lucius*]; mud-eel, (?) [lamprey?]; silver-eel, (*Anguilla rostrata*) [American eel]; buffalo fish, (*Bubalichthys bubalus*) [buffalo, *Ictiobus* ____?]; red horse, (*Myxostoma macrolepidota*) [shorthead redhorse, *Moxostoma macrolepidotum*]; suckers, *Catostomus* ____?]; bull-heads, (*Amiurus catus*) [bullhead, *Ictalurus* ____?]; spoon-fish, or shovel-bill, (*Polyodon folium*) [paddlefish, *Polyodon spathula*]; sun-fish, (*Pomotis* ____?) [sun-fishes, *Lepomis* ____?]; cat-fish, (*Amiurus* ____?) [catfish, *Ictalurus* ____?]; dog-fish, (*Amia calva*) [bowfin]; gar pike, (*Lepidosteus osseus*) [longnose gar, *Lepisosteus osseus*]; perch, (*Perca americana*) [yellow perch, *Perca flavescens*], were caught in both these rivers, and also in the Du Page River, which flows 6 miles east of Joliet, and empties into the Desplaines 8 miles south of that town; also in Hickory Creek, which rises about 14 miles east of Joliet, and empties into the Desplaines just south of the town, and in any of the streams of sufficient size in this vicinity.

"When the current of Chicago River was first turned through the canal and the rivers, it caused the fish in them to bloat to a large size, and rising to the surface they floated down the stream in large numbers. It was estimated at the time that several tons of dead fish passed through one of the canal locks just after the foul water commenced running through the canal.

"When these bloated fish chanced to float into the clear water at the mouth of some tributary of the river they would revive and swim up the clear stream. Such large numbers of the fish revived in this manner that all the small streams flowing into the Desplaines and Kankaku [*sic*] rivers were filled with fish in such numbers that many were taken with hook and line, one man taking over 300 in a day in this manner at that time.

"When the spring freshets occur the current is so rapid and the amount of pure water in the river is so great, that the foul water does not have much effect upon the fishes, and large numbers of the species mentioned ascend the rivers and are caught with hook and line. Later in the season as the water subsides, and the water from Chicago River predominates, the fish which came up in the spring die and are floated down the river. In July and August when the water is the worst even the mud turtles leave the river in disgust and seek less odorous homes."

Water from the Illinois-Michigan Canal also entered the Illinois River at La Salle (mile 223), but the wastes were sufficiently decomposed at that point that there was only a slight impact on the ecosystem of the Illinois River below La Salle (Starrett 1972: 145).

The carp was introduced into the Illinois River in 1885, out of a stock brought to the United States a few

years earlier from Europe (Forbes & Richardson 1920:105). By 1898, the carp catch exceeded the value of all other commercial fishes from the Illinois River (Thompson 1928:285). Forbes & Richardson (1920:108-109) reported fishery statistics which showed that increasing carp populations did not adversely affect the populations of other species, although they did predict that carp might displace the native buffalo fishes, which have the same food preferences as carp. Forbes & Richardson (1920: 108-110) did not feel that carp had increased the turbidity of the water in the Illinois River by their rooting habit of bottom feeding. In contrast, Jackson & Starrett (1959:163-165) observed local areas of heavy turbidity in Lake Chautauqua, a bottomland lake along the middle section of the river, produced by schools of carp. They felt that some instances of carp activity may have been stimulated by low oxygen levels. The activities of carp may have had a greater effect on turbidity in more recent times because of the presence of flocculent bottom muds that have been carried into the bottomland lakes by the river (Starrett & Fritz 1965:88).

Forbes (1928) does not mention any changes in fish fauna associated with the construction, prior to 1900, of the low navigation dams on the Illinois River at Marseilles, Henry, Copperas Creek, La Grange, and Kampsville. Nelson (1878:798) was of the opinion that a dam at Seneca (mile 252.5) hindered the upstream movement of fishes. On 1 January, 1900, the Sanitary and Ship Canal was opened at Chicago, connecting the Des Plaines and Illinois Rivers with Lake Michigan. The canal was used to flush municipal and industrial wastes into the Illinois River system, and away from Chicago's municipal water intakes in Lake Michigan. The quantity and quality of this diverted water had a tremendous impact on the Illinois

River. There was an average rise in water levels at Havana of 2.8 feet (.85 m), and during the normal low-flow period between June and September the rise was 3.6 feet (1.10 m) (Forbes & Richardson 1919:140-141). The tree line along the river retreated as a result, and the loss of mature pin oak (*Quercus palustris*) and pecan (*Carya illinoensis*) trees meant a loss of food for mallard ducks (*Anus platyrhynchos*) and wood ducks (*Aix sponsa*) (Mills, Starrett, & Bellrose 1966:5). Populations of cavity-nesting tree swallows (*Iridoprocne bicolor*) and prothonotary warblers (*Protonotaria citrea*) increased, as a result of the increased supply of nest sites in zones of dead trees bordering the river and lakes. Populations of these species declined markedly during the 1940's, as the last of the dead trees finally collapsed (Dr. Frank C. Bellrose, Waterfowl Biologist, Illinois Natural History Survey, personal communication).

One beneficial effect of the diversion was to increase the surface area of water in lakes and backwaters, which apparently improved the fishery (Forbes & Richardson 1919). It is also likely that the stumps and snags left after the trees had died temporarily provided cover for certain species such as bass, crappie, and other sunfishes. The increased shallow water areas and nutrient loading of the Illinois River and its bottomland lakes initially may have increased the plankton populations and the biomass of bottom fauna in the middle and lower river (Forbes & Richardson 1913:494-495). In the river proper, populations of molluscs, especially fingernail clams, probably increased the most, with a beneficial effect on mollusc-consuming species of adult fish such as carp, catfish, buffalo, and drum.

After approximately 1910, however, as the pollution load increased, critically low dissolved oxygen levels oc-

curred farther and farther downstream with detrimental effects on food organisms and fish (Richardson 1921b:33). Populations of molluscs, including fingernail clams (*Sphaeriidae*), in the middle section of the Illinois River and in several bottomland lakes were quite high in the early 1950's (Paloumpis & Starrett 1960).

In 1938, by order of the Supreme Court of the United States, the amount of water that could be diverted from Lake Michigan at Chicago was limited to a yearly average of 42.48 m³/sec and minimum gage readings in the middle section of the river at Havana dropped about .61 m as a result (Starrett 1972:146). In spite of an increasing human population in the Illinois basin, the population equivalent of the total combined domestic and industrial waste emptied into the river declined from 6,211,471 in 1922 to 2,417,000 in 1960 (Mills, Starrett, & Bellrose 1966:9), because more waste was receiving primary and secondary waste treatment. Population equivalents are based on the average amount of carbonaceous oxygen demand in the waste produced per person, and do not take into account the oxygen demand of the nitrogenous fraction of human waste. The demand placed on the oxygen resources of the river by nitrogenous wastes has actually increased in recent years (Butts 1975).

Minimum dissolved oxygen levels near the surface in the channel of the Illinois River during midsummer in the period 1911-1966 are reported in tables in Mills, Starrett, & Bellrose (1966:9) and Starrett (1971:370-373). In 1966, oxygen levels generally were below saturation throughout the whole length of the river. Levels below 1.0 mg/l occurred in Dresden, Peoria, and La Grange Pools. The reduction in dissolved oxygen concentration so far downstream of the Chicago and Peoria metropolitan areas results from the oxygen demand of sediment (Butts

1974) and from the oxygen demand as ammonia in municipal waste is converted to nitrate (Butts 1975). During the winter, bacterial nitrification is slowed, oxygen demand is thereby reduced, and higher ammonia concentrations extend farther downstream from Chicago (Butts 1975).

Ammonia places aquatic organisms in double jeopardy; it not only removes oxygen from water, but is also toxic. Only the un-ionized fraction of the total ammonia concentration (approximately 5 percent of the total ammonia in the Illinois River) is toxic, and the un-ionized ammonia concentrations were generally well below lethal levels for fish in 1972 and 1973, although concentrations may have been high enough on occasion in the upper river to stress fish (Lubinski et al. 1974).

It is not known to what extent the low dissolved oxygen concentrations, perhaps acting in combination with other stresses such as silt and toxic materials, contributed to the die-off of fingernail clams and snails in the middle section of the river in the mid-1950's (Mills, Starrett, & Bellrose 1966: 12). As late as 1973, fingernail clams had not reappeared in areas of the river where dead shells indicated that they were formerly abundant. The loss of these important food organisms, according to the Mills, Starrett, and Bellrose report, has resulted in a reduction of the number of diving ducks migrating along the Illinois River and a decline in the condition factor of the commercially valuable carp.

In addition to affecting the food supply of fish, low oxygen levels have direct effects on fish. Carlson & Siefert (1974) have shown that oxygen levels at 35 percent saturation reduced the survival of larval largemouth bass by 13.7 percent, and oxygen levels at 70 percent saturation and below retarded the growth of larval bass. In two areas that provide good physical conditions for largemouth bass, Lower Bath Chute,

La Grange Pool (Fig. 9) and Chillicothe Island Chute, Peoria Pool (Fig. 10), midsummer oxygen levels were at 35 percent saturation or below for 4-5 years out of the 8-year period 1963-1970.

The discharge and water levels were generally high preceding the resurgence in bass populations at Lower Bath Chute (Fig. 9). Therefore, it is difficult to separate the beneficial effects of high water levels from the beneficial effects of increased discharge. During high water, flooded areas provide good breeding habitat for many adult fish and good nursery areas for juvenile fish. High discharge results in increased dilution of toxic wastes and oxygen-demanding wastes. At Chillicothe Island Chute (Fig. 10) the relative importance of the two effects can be separated, because the water levels in Peoria Pool were maintained within fairly narrow limits by flow regulation at the Peoria Lock and Dam, while the discharge varied considerably.

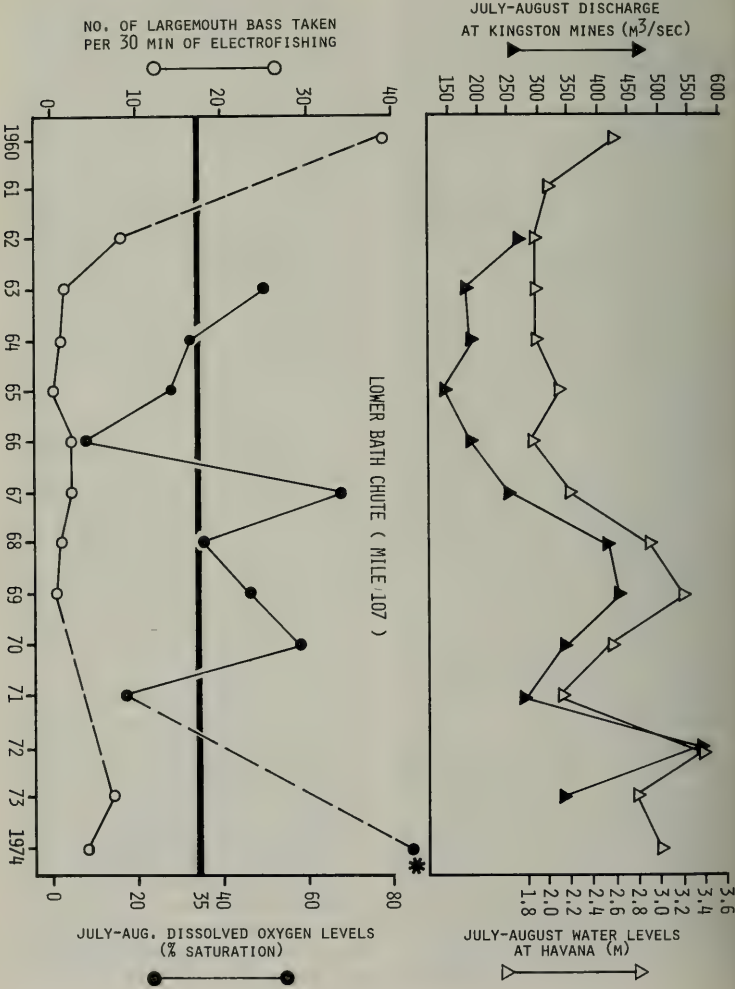
The resurgence in bass populations at Chillicothe Island Chute was associated with increased discharge. Although we took no oxygen readings in the chute during midsummer 1973 or 1974, oxygen readings in other parts of the river were generally 80 percent of saturation, and indicate that oxygen-demanding wastes were being diluted. Toxic wastes probably were diluted during this period also.

Lubinski et al. (1974) indicated that the combined toxicity of the chemicals routinely monitored by the Illinois Environmental Protection Agency was generally well below levels lethal to fish at 17 locations on the Illinois River during an 18-month period in 1972 and 1973, when discharge was high. Extensive monitoring of toxic materials in the Illinois River has been undertaken only recently, so Lubinski et al. (1974) were not able to estimate the combined toxicity of chemicals to fish during low discharge. The real

test of whether pollution abatement programs in the Illinois Valley have resulted in improvement of water quality for fish will occur during low discharge periods in the years to come.

One of the major impacts on the

Illinois River below Hennepin was the leveeing and draining of bottomland areas, primarily in the period 1903-1926. Of 400,000 bottomland acres (161,874 ha) subject to overflow by the river, approximately 200,000



acres (80,937 ha) are now behind levees (Mills, Starrett, & Bellrose 1966: 5), with a consequent reduction in wildlife and fish habitat. The backwaters and bottomland lakes of the Illinois River were, and are, critically important to fish and wildlife production.

Richardson (1921a:464) reported that the largest weights of fish per acre were taken in reaches of the river with the largest connecting lake area:

"Taking the year 1908 as an illustration, and using the figures for separate shipping points obtained by the Illinois Fish Commission in that year, we find for the 59.3 miles of river and lakes between Copperas Creek dam (river mile 136.9) and La Grange dam (river mile 77.6), with about 90% of its acreage consisting of lakes and ponds, an average fish-yield per acre for water levels prevailing half the year, of 178.4 pounds; for the 87 miles from La Salle (river mile 223.9) to Copperas Creek dam, with about 83% lakes, 130.4 pounds; and for the lower 77 miles, La Grange to Grafton, with around 63% lakes, only 69.8 pounds."

Richardson (1921a:463) indicates that well over 80 percent of the total fish yield in 1908 came from the lakes, with much less than 20 percent coming from the river itself. The bottomland lakes supported an abundant aquatic weed-inhabiting invertebrate fauna, which supplied food for young fishes of the sunfish, perch, and pike families.

In the 1930's high navigation dams were constructed at Dresden Heights (6.71 m high), Marseilles (7.32 m),

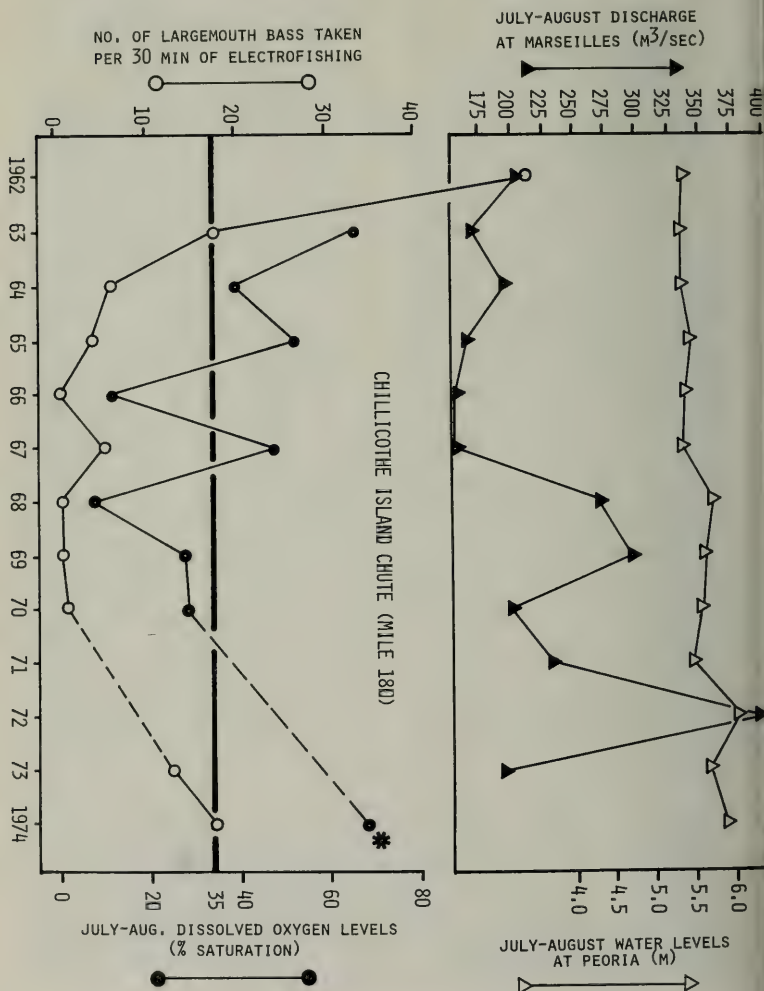
Starved Rock (5.79 m), Peoria (3.35 m), and La Grange (3.05 m). The navigation dam at Alton on the Mississippi raised water levels in the Illinois as far north as Hardin, at river mile 21.0. Timber and brush were cleared from areas due to be inundated by the new dams. Clearing operations probably did not markedly reduce the amount of mast available for waterfowl, according to Dr. Frank C. Bellrose, Waterfowl Biologist, Illinois Natural History Survey. The navigation dams temporarily increase dissolved oxygen levels as the water passes over and through the dams (Mills, Starrett, & Bellrose 1966:9-10; Forbes & Richardson 1913:549). Starrett (1971:271-272) indicated that the reduction of diversion from Lake Michigan coupled with the higher dams on the river have resulted in a decrease of average current velocity from about 2.01-4.02 km/hour prior to 1908 to 0.97 km/hour in 1966. Pools behind navigation dams on the upper river have filled with oxygen-demanding sediment which in places resembles sludge from secondary sewage treatment plants (Butts 1974).

Richardson (1921a:457, 474-475) indicated that abundant populations of fingernail clams in the Illinois River were generally found in areas of reduced current and favorable conditions for sedimentation. We (and others, such as Gale 1969) have found that abundant populations of fingernail clams occur in Pool 19 on the Mississippi River, over soft mud bottoms, and Gale (1971) reported that fingernail clams will select mud substrates in preference to sandy mud and sand.

Fig. 9.—The relationships among mean water levels (open triangles), mean discharge (black triangles), and mean dissolved oxygen levels (black dots) during the months of July and August and the number of largemouth bass taken per 30 minutes of electrofishing (circles) in the fall at Lower Bath Chute (mile 107) in the La Grange Pool. Oxygen levels below 35 percent saturation (heavy line) reduce the survival of larval largemouth bass. Discharge was measured at Kingston Mines (mile 145), water levels at Havana (mile 120), and oxygen levels in the chute. The oxygen reading marked by an asterisk was taken on 12 September, rather than in midsummer. Discharge rates were obtained from **Water Resources Data for Illinois**, U.S. Dept. of the Interior, Geological Survey. Water levels were obtained from **Missouri-Mississippi River Summary & Forecasts**, U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Weather Service Central Region, Kansas City, Missouri. The other data were obtained by the Illinois Natural History Survey.

If the high navigation dams constructed in the 1930's did reduce the current and increase sedimentation in parts of the Illinois River, then the habitat suitable for fingernail clams may have increased, with a benefit to the mollusc-

eating fish. It is puzzling that conditions have been so dramatically different since 1955, when a die-off of fingernail clams occurred in the middle section of the Illinois River (Mills, Starrett, & Bellrose 1966:12). As late as



1973, the fingernail clams had not returned to areas of the river where dead shells indicated they had formerly been abundant.

Starrett (1971:272) felt that the increase in sluggishness of the river and the increased planting of row crops in the Illinois basin have made siltation in the last 30 years an important factor adversely affecting the survival of mussels and other organisms in the Illinois River and its bottomland lakes. Silt physically removes habitat by filling in areas such as Lake Chautauqua, near Havana (river mile 124-130), which has lost 18.3 percent of its storage capacity in a period of 23.8 years (Stall & Melsted 1951:1). Areas in Quiver Lake near Havana where boats could formerly be launched are now only a few centimeters deep in low water stages, and willows are encroaching on the lake. Jackson & Starrett (1959:160) stated:

"The sediments in Lake Chautauqua are mostly of a fine texture and form a loose, flocculent 'false bottom' (not similar to the type found in bog lakes) over the original lake bottom. A slight disturbance of the 'false bottom' causes particles to become resuspended and so increases the turbidity of the water."

The same authors found that an increase in wind velocity from light to strong increased the turbidity from 162 to 700 Jackson turbidimeter units (JTU) and that it took a calm period of 7-12 days for much of this sediment to settle from Lake Chautauqua. As a consequence, this lake and other bottomland lakes are highly turbid most of the time.

The turbidity levels in bottomland

lakes and backwaters along the Illinois River are within the range that reduces fish production. Buck (1956) studied fish production in farm ponds, hatchery ponds, and reservoirs in Oklahoma which had a wide range of turbidities. The farm ponds were treated with rotenone, then restocked with largemouth bass and bluegills or largemouth bass and redear sunfish (*Lepomis microlophus*). Twelve farm ponds were divided into three turbidity classes. After two growing seasons, the average total weights of fish were:

Clear ponds

(less than 25 JTU)—161.5 lb/acre
(181.0 kg/ha)

Intermediate ponds

(25-100 JTU)—94.0 lb/acre
(105.4 kg/ha)

Muddy ponds

(>100 JTU)—29.3 lb/acre
(32.8 kg/ha)

The decline in production in turbid ponds resulted from a decline in both reproduction and growth (Buck 1956).

The results from hatchery ponds, where turbidities were artificially controlled, and from the reservoirs which harbored a variety of fishes, generally paralleled the results from the farm ponds, except for two species, channel catfish and flathead catfish.

Channel catfish spawn in dark cavities, such as hollow logs or in holes in banks. Turbid waters are likely to have more suitably dark cavities per surface area or length of shoreline than do clear waters, and thus reproduction of channel catfish was probably greater in the turbid waters. Flathead catfish grow well in turbid waters and appear to be well adapted to turbid conditions.

Fig. 10.—The relationships among mean water levels (symbols are the same as in Fig. 9), mean discharge, and mean dissolved oxygen levels during the months of July and August and the number of largemouth bass taken per 30 minutes of electrofishing in the fall at Chillicothe Island Chute (mile 180) on the Illinois River. Oxygen levels below 35 percent saturation (heavy line) reduce the survival of larval largemouth bass. Chillicothe Island Chute is in the Peoria Pool. Discharge was measured at Marseilles (mile 247), water levels at Peoria (mile 163), and oxygen levels in the chute. The oxygen reading marked by an asterisk was taken on 30 September, rather than in midsummer. Data were obtained from the same sources as given for Fig. 9.

Buck (1956:257) concludes that in newly formed reservoirs bass, crappies, and other scaled fish out-produce catfish and then limit them by predation on the young. Turbid waters offer catfish protection from these predators. In addition, sunfishes prefer to construct nests on firm substrates, rather than mud. Their eggs and fry are probably more susceptible to smothering by sediment than those of catfish and rough fish.

The disappearance of the yellow perch (*Perca flavescens*) from the Illinois River and its bottomland lakes is probably also associated with the disappearance of the plant beds and clean sandy or pebbly bottoms the perch uses for spawning.

Catfish feed on the types of food organisms which can grow in turbid waters with mud bottoms, such as midges, worms, fingernail clams, and snails. Catfish can use their highly developed sense of smell to locate food, whereas other game fish rely more heavily on sight. Food habits studies have shown that young game fish feed first on zooplankton, then on insects such as dragonfly and damselfly nymphs, then on larger organisms such as fishes and crayfishes. These types of food organisms are associated with weed beds and moderately clear water. The bottomland lakes along the Illinois River have been transformed from the latter type of ecosystem to a turbid type of system, by the influx of sediment from the river.

Recently, even the fish and duck food organisms which are adapted to mud bottoms have died out in the channel and lateral areas of the middle section of the Illinois. Fingernail clams in this section died out in 1955, and have not since recolonized the area. It is possible that some of the heavier benthic animals such as the molluscs find it difficult to remain near the top of the flocculent bottoms or that the suspended material interferes with their

feeding activities. The senior author suspects that the sediments exert an oxygen demand in the lakes, just as they do in the river. In August, 1974 dissolved oxygen levels in Meredosia Lake (river mile 72-77) were approximately 3 mg/l when a strong wind was blowing that stirred bottom sediments in the shallow lake. A die-off of gizzard shad was occurring, and almost all the fingernail clams maintained in plastic cages on the bottom of the lake had died since they were last checked in mid-July. Oxygen levels may have been lower than 3 mg/l on previous occasions. Oxygen levels in the river on the same date were approximately 6 mg/l. It is also possible that toxic materials, such as pesticides, that are bound to soil particles, were taken up by aquatic organisms such as clams that ingested the soil particles or passed them over their respiratory membranes. In addition, toxicants such as hydrogen sulfide may have been formed and released from bottom muds under anaerobic conditions.

The increased barge traffic (Starrett 1972:153) associated with the improved navigation channel increases the turbidity of the river. The turbulence produced in midchannel, as well as the washing action along shore, resuspends sediment, thereby increasing the turbidity (Fig. 1 and 2). W. C. Starrett made numerous observations of the effect of barges on turbidity of the river, for example (Starrett 1971:273):

"A towboat underway causes a strong current and washing action on the silt bottom ("false bottom") inshore, which resuspends the silt particles, thereby increasing the turbidity. The increase in turbidity is more noticeable in the lower three pools, particularly in the Alton Pool, than it is upstream because of differences in bottom types. . . . The outrush of water from shore toward the channel caused by a towboat also temporarily exposes the shallow areas. On November 18, 1964, in the Alton Pool at river mile 65.1,

the turbidity just prior to the passing of two towboats was 108 units (Jackson turbidity units), and within 6 minutes after the tows had passed, the turbidity was 320 units. Sixteen minutes later the turbidity had dropped to 240 units."

Some personal observations were made on the effects of towboats during the 1974 electrofishing investigations. On several occasions, flow reversals in chutes were observed as tows passed first one end, then the other, of a chute. In a narrow part of the river channel above Pekin on 19 September, 1974, in the midst of electrofishing, our boat was stranded on the mud when the water rushed out from shore as a tow of nine fully loaded coal barges passed upstream. Mussel shells were clearly visible on the bottom for several seconds before the water rushed back again. We had been in approximately 0.5 m of water.

Such washing along the shore and flow reversals in side channels may have a detrimental effect on benthic organisms and fishes that make nests in shallow water, such as sunfishes.

Low flows from 1962 to 1964, and consequent low oxygen levels and reduced dilution of toxic wastes, apparently are responsible for the decline during the same period of game species such as largemouth bass, crappies, and bluegill. Catches of these species showed dramatic recoveries following the high-water period 1971-1973. In 14 years of electrofishing, covering the period 1959-1974, the largest numbers of the following species were obtained in 1974, following the high water period: black crappie, white crappie, flathead catfish, white bass, bluegill, bigmouth buffalo, and black buffalo. The maximum weights of the following species were obtained in 1974: white crappie, channel catfish, and bluegill. Fig. 8, 9, and 10 show that bass populations still had not recovered to the peak levels observed in Peoria and La Grange Pools in the years 1959-1962.

High water levels stimulate certain species, such as white bass, to run up tributary streams and spawn. White bass were obtained in the upstream pools, Starved Rock and Marseilles, in fairly substantial numbers in 1973 and 1974, whereas none were obtained in these pools in 1959, 1961, 1963, 1964, 1968, and 1969. High water also increases the space available for spawning activities of fishes that build nests in shallow water, such as sunfishes, and the amount of protected habitat available for juvenile fish, in shallow, flooded areas and around brush and tree stumps. As mentioned above, higher oxygen levels have occurred in the Illinois River in association with the high flows, with beneficial effects on fish and fish food organisms.

In spite of the improvement in the electrofishing catch in 1973 and 1974, apparently due to high water levels in 1971-1973, the commercial catch of fish in the Illinois River continued its historical decline in the 1970's (Table 28). Depending on whether the Illinois Department of Conservation figures or the National Marine Fisheries Service statistics are used, the catch dipped under 1 million pounds (454,000 kg) in 1971 or 1972. The decline is not explained by a reduction in the number of commercial fishermen—there were 13 full time and 56 part time Illinois River commercial fishermen in 1973, and 9 full time and 47 part time in 1971. Nor is it explained by a decline in economic value of the catch. The catch from the Mississippi River bordering Illinois has been relatively constant from 1950 through 1973 (Table 28). A general decline in profits would be reflected in a general decline in fishing effort in both the Illinois and Mississippi Rivers and a corresponding decline in catch. It is possible that because fishermen generally take large adult fish, an increase in the catch of commercially important sizes of fish will not be seen until the fish spawned in 1973 and 1974 reach marketable size.

FUTURE IMPACTS ON THE FISH POPULATIONS OF THE ILLINOIS RIVER

In 1971 the Chicago Metropolitan Sanitary District began a large-scale sludge recycling project near the Illinois River at St. David. In 1974, the District began aerating a section of the Chicago Sanitary and Ship Canal, and more of the canal will be aerated in succeeding years. In the future, all Chicago storm water probably will be captured and stored in a deep tunnel under Chicago, instead of being discharged into the canal, and will be treated before it is released to the canal. Advanced waste treatment plants should be capable of removing the ammonia that now exerts an oxygen demand so far down river. All of these improvements in waste treatment will have a beneficial impact on the aquatic life in the river, by reducing the oxygen demand on the river and improving oxygen levels during critical low-flow periods. Waste treatment probably will also be improved in the Pekin-Peoria metropolitan area.

A proposed increase in the depth of the navigation channel of the Illinois River (from 2.7 to 3.7 m), would be accomplished by a combination of raising low-flow water levels and dredging. Depending on local topography, the water surface area might be increased. Judging by the increased fishery in the Illinois River following a rise in water levels in 1900, as a result of water diversion from Lake Michigan, one might expect a beneficial effect. However, bottomland lakes that now have a chance to clear during periods when they are cut off from the river might then become permanently connected to the river and receive a continuous, rather than intermittent, input of oxygen-demanding sediment. In 1921, Richardson (1921a:418) reported that Quiver Lake (mile 121.0-mile 124.0) and Matanzas Lake (mile 114.5-117.0) received spring water from the sandy

bluffs on the east side, and that the waters in these lakes were somewhat clearer than in other bottomland lakes. According to an Illinois Water Survey report (Singh & Stall 1973:19), the influx of ground water to the river from Kingston Mines (mile 145.3) to Moredosia (mile 71.1) amounts to 8.75 m³/sec, or about one-twelfth of the total input to this section of the river, during the lowest flow expected for a 7-day period at a recurrence interval of 10 years. According to Matanzas Beach residents, the water and shoreline of Lake Matanzas still are cleared of silt deposited by the river, due to the flushing action of ground water coming through the sandy bottom along the bluff. In contrast, Quiver Lake is now filled with silt.

The Illinois Department of Conservation has been able to restore aquatic vegetation to Rice Lake (mile 133-137) and Stump Lake (approximately mile 5) by pumping water out of the lakes or allowing them to dry out naturally (personal communication, Robert L. Glesenkamp, Area Wildlife Manager, Illinois Department of Conservation). Midsummer drying was a natural occurrence in this type of shallow lake, during low-flow years, prior to Lake Michigan diversion and construction of navigation dams (Richardson 1921a:419). On drying, the bottom muds were compacted, and when the lakes were reflooded, the turbid water generally cleared, and the plants gained root-hold in the firm bottom. Restoration efforts would be more difficult if summer water levels were higher. In addition, private duck clubs and state and federal wildlife refuges along the river would find it difficult to reduce water levels. They attempt to reduce water levels to expose mud flats and encourage the growth of moist-soil food plants for waterfowl. Once again, a natural drying cycle has had to be replaced or supplemented by pumping, because water levels do not attain the low

levels they once did. Such management techniques require energy, equipment, and manpower.

Larger towboats using the improved navigation channel and an increased number of towboats would keep more silt in suspension and increase the washing action along the shore and flow reversals in chutes. Fig. 1 shows that if towboats pass a point in the river more frequently than once every 2½ hours, the resuspended sediment will not have a chance to settle out and the average amount of sediment suspended in the water will increase with a consequent increase in oxygen demand and turbidity. The more silt there is in suspension in the river, the faster bottomland lakes such as Lake Chautauqua (mile 124-130) will fill with oxygen-demanding sediment, as they are periodically overflowed by the river.

The effect of various future channel improvement schemes and various levels of boat traffic on the siltation rate in the critical backwater areas and lakes needs to be predicted. In addition, the joint effects of man's activities in the river and drainage basin needs to be assessed. For example, it is possible that the proposed increase in diversion of Lake Michigan water at Chicago (discussed in more detail below) may make it possible for the present channel to accommodate deeper-draft barges in certain areas, without additional dredging or higher dams.

It would be counter-productive for one arm of government to spend resources in improving and restoring refuge areas if another arm of government engages in practices which degrade such areas. There will be little benefit to the fisheries of the Illinois River by having the Chicago Metropolitan Sanitary District and other municipalities and industries expend billions of dollars in improved waste treatment if the river and its bottomland lakes are increasingly degraded by silt. Refuges, unpolluted lakes, and

unpolluted tributary streams must be maintained if the river is to show the recovery pattern in the future that it exhibited in 1973-1974, following the high-water period and improved oxygen levels from 1971-1973. When formerly degraded areas are restored, they can be recolonized rapidly by species that are desirable to man, if reservoirs of such species, and reservoirs of food organisms for desirable species, are available in undegraded pockets in the ecosystem. In a properly functioning system, the refuges maintained by man have precisely this function.

The most practicable solution to the silt problem may be to reduce the amount entering the river in the first place, if predictive studies indicate that a reduction of silt input would actually reduce siltation in the lakes and backwaters. Once the silt is in the river and lakes, it may be recycled and resuspended there, and it is possible that no reduction in turbidity or oxygen demand would be achieved by reduction of silt input without the use of restoration techniques, such as drying out of lakes. On the other hand, it is possible that reduced silt input may cause the river to flush out backwater areas and lakes during periods of high flow, thus bringing about a natural restoration of these areas. Once the turbidity was reduced, fringing marshes and beds of aquatic plants might appear again, further accelerating restoration by acting as silt filters and nutrient traps.

The silt entering the river could be reduced by wide adoption of soil conservation practices in the Illinois basin, including such new practices as no-till farming, where row crops are planted without greatly disturbing the soil. Before the latter practice is adopted on a wide scale, the total energy requirements (including the energy for the manufacture of agricultural chemicals) of various alternative farming methods need to be determined, and the en-

vironmental impact of the herbicides that must be used with present no-till farming methods needs to be assessed.

The City of Chicago and lakefront residents whose property has been damaged as a result of current high water levels in Lake Michigan have requested an increased diversion of Lake Michigan water into the Illinois River. An increased diversion would probably raise water levels, with some of the detrimental effects discussed above. However, Lake Michigan water is good quality water and probably would improve the quality of the upper river by a simple dilution, if diversion occurred during the summer months. On the other hand, if ammonia removal is not achieved by the Chicago Metropolitan Sanitary District, the effect of increased diversion might be to push this oxygen-demanding waste farther downstream before its oxygen demand could be satisfied.

Two introduced species have entered the Illinois River recently and will probably become more abundant, just as the introduced carp, goldfish, and white catfish have. It is difficult to predict whether the latest arrivals will increase explosively, as carp and goldfish did, or whether they will barely maintain themselves, as white catfish have. White catfish are only occasionally taken from the Illinois River and do not seem to reproduce abundantly in the river. The white amur (*Ctenopharyngodon idella*), a plant-eating fish introduced from Asia, is now being taken regularly by commercial fishermen from the Mississippi River at Crystal City, Missouri and from the Missouri River (Personal communications, William L. Pflieger, Fishery Biologist, Missouri Department of Conservation, and Peter Paladino, District Fishery Biologist, Illinois Department of Conservation), and has probably entered the lower Illinois River. If rooted aquatic vegetation could be restored to the Illinois River and its bottomland lakes by the lake

restoration techniques discussed above, or by a reduction of silt loads in the river as a result of improved soil conservation practices in the basin, the white amur might have a detrimental impact. On the other hand, white amur from the Mississippi are being marketed in small quantities commercially and their flavor is reported to be excellent. White amur in the Mississippi grow to a large size (4.5–6.4 kg) in 2 years (Personal communications, Pflieger and Paladino). They might become a useful commercial species in the Illinois River.

Another exotic species, the Asiatic clam (*Corbicula manilensis*) was found at three locations on the Illinois in the course of the 1974 electrofishing survey: at Kampsville (river mile 32.0), Bath Chute (mile 106.7), and Turkey Island Chute (mile 148.4) (Thompson & Sparks, in press). The Asiatic clam is a serious nuisance, because it has blocked condenser tubes of power plants in Illinois and elsewhere. In addition, it may displace the native fingernail clams.

The future of the Illinois River will largely be determined by man's activities in the river and adjacent floodplain and by his use of the land in the drainage basin. Predictions of the impacts of various activities must be developed, so a rational management scheme for the Illinois River can be designed and the river can continue to serve a variety of purposes in the future.

SUMMARY

1. The upper Illinois River is warmer than the lower River, as a result of warm municipal and industrial effluents.

2. The upper river is less turbid, because the bottom is generally rocky, whereas Peoria, La Grange, and Alton Pools contain flocculent muds that have entered the river and are kept in suspension by the river current and by

wave action resulting from wind, tow-boats, and pleasurecraft.

3. Dissolved oxygen levels at the surface and the bottom of the river were virtually the same in the fall of 1974, and dissolved oxygen levels were 77–97 percent of saturation in Alton Pool, 65–122 percent of saturation in La Grange and Peoria Pools, and 47–104 percent of saturation in the upper Pools of Starved Rock, Marseilles, and Dresden. Local areas of super-saturation occurred where plankton blooms appeared to be in progress. In two areas that provided good physical habitat for largemouth bass, Lower Bath Chute, La Grange Pool (mile 107) and Chilli-cothe Island Chute, Peoria Pool (mile 180), midsummer oxygen levels were at 35 percent saturation or below for 4–5 years out of the 8-year period 1963–1970. Laboratory experiments have shown that oxygen levels below 35 percent saturation reduce the survival of larval largemouth bass and levels below 70 percent retard their growth.

4. The number of fish species taken by electrofishing in the Dresden Pool, Des Plaines River portion of the Illinois Waterway during the period 1959–1974 was consistently low (Tables 29 and 30). Only carp and goldfish and hybrids of these two pollution-tolerant species were commonly taken.

5. The following species showed a trend of increasing abundance in the downstream direction, away from Chicago, with the largest number occurring in Alton Pool: shortnose gar, bowfin, goldeye, mooneye, channel catfish, flathead catfish, and white bass.

6. Goldfish showed a trend of increasing abundance in the upstream direction, toward Chicago.

7. The following species were most abundant in one or both of the two middle pools of the river, La Grange and Peoria Pools, which have the most connecting lake area: gizzard shad, carp, river carpsucker, smallmouth buf-

falo, bigmouth buffalo, black buffalo, yellow bullhead, green sunfish, bluegill, largemouth bass, white crappie, black crappie, and freshwater drum.

8. Gizzard shad and carp were generally abundant throughout the river.

9. Black bullheads were abundant at one atypical station, Ballard Island Chute, Marseilles Pool (mile 247.8–248.2), which apparently provides preferred habitat for this species.

10. Gamefish populations declined during the low water years 1962–1964, and recovered following the high water years 1971–1973. Largemouth bass populations did not recover to 1959–1962 levels. The recovery appears attributable to improved oxygen levels in the river, and perhaps to increased dilution of toxic materials, and demonstrates how rapidly fish populations respond to improved conditions in the river.

11. The commercial and sport fisheries in the Illinois River have generally declined from levels around the turn of the century. The decline is attributable to a loss of habitat and increasing pollution. Habitat was lost due to leveeing and draining of bottomland areas in the period 1903–1926 and due to sedimentation in the remaining areas. Sedimentation has resulted in undesirable habitat modification, as well as habitat reduction.

12. Northern pike, yellow perch, and walleye (*Stizostedion vitreum vitreum*) were once abundant in the river but are now rare or limited in their distribution. Yellow perch populations have declined probably as the result of the disappearance of beds of aquatic plants and disappearance of clean sand or pebble substrates perch use for spawning.

13. In the past the bottomland lakes and backwater areas offered havens for fish and fish food organisms, as the river became increasingly polluted. Now dissolved oxygen levels in the river seem to have improved, while

the lakes have filled with sediment that apparently exerts an oxygen demand, keeps aquatic plants from growing, and does not support an abundance of food organisms.

14. More and better waste treatment facilities are being constructed by industries and municipalities in the drainage basin of the Illinois River. However, the production of fish and wildlife in the Illinois River and its bottomland lakes is not likely to improve unless sediment pollution is also brought under control.

15. The consequences of future uses of land in the drainage basin and the consequences of future uses of the river must be predicted, so that a wise selection of alternatives can be made. If the river is to be managed in the future for a variety of beneficial uses, then the various state, federal, and private agencies charged with managing land and water within the drainage basin must work in a coordinated fashion, rather than at cross purposes.

GUIDE FOR USE OF TABLES OF ELECTROFISHING RESULTS (Tables 3-27)

SYMBOL	EXPLANATION
1	Dresden Pool, Des Plaines River—not included in tabulated value for the Illinois River at bottom of each table.
2	Values represent the total number of fish or total weight

of fish taken during the designated year in the Illinois River divided by the number of half-hour intervals fished. Illinois River pools are Alton, La Grange, Peoria, Starved Rock and Marseilles. The Dresden Pool, Des Plaines River, is excluded from this tabulation.

Denotes less than 0.01 kilograms or fish per 30 minutes fished.

Note: Fish species are listed in phylogenetic order. All common and scientific names are taken from *A List of Common and Scientific Names of Fishes from the United States and Canada*, 3rd edition, 1970, American Fisheries Society Special Publication No. 6. Species that were rarely taken by electrofishing are not shown in the tables, but are discussed in the text. The values in the body of each table are determined by summing the number of fish or weight of fish obtained at all stations in the navigation pool and dividing the sum by the total number of half-hour intervals fished in that pool. Thus the values are average catches per unit effort for each pool. The number of electrofishing stations in each pool are as follows: Alton Pool (4-5), La Grange Pool (6), Peoria Pool (8), Starved Rock Pool (2), Marseilles Pool (3), and Dresden Pool (1).

Table 1.—Illinois Natural History Survey electrofishing sites on the Illinois Waterway, 1959–1974.

<i>Pool</i>	<i>Station</i>	<i>River Mile^a</i>
Alton	Mortland Island Chute	
	Below Hardin	18.7–19.4
	Diamond Island Chute	
	Above Hardin	24.0–25.5
	Hurricane Island Chute	
	Above Hardin	26.0–27.2
	Crater Island and Willow Island Chutes	
	Below Kampsville	29.3–30.7
	Big Blue Island Chute ^b	
	Above Florence	57.5–58.9
La Grange	Bar Island and Grape Island Chutes	
	Below Beardstown	86.2–87.1
	Sugar Creek Island Chute	
	Below Browning	94.3–95.2
	Lower Bath Chute	
	Above Browning	106.8–107.5
	Upper Bath Chute	
	Above Bath	112.8–113.3
	Turkey Island Chute	
	Above Kingston Mines	147.3–148.2
Peoria	Illinois River	
	Above Pekin	154.5–155.3
Peoria	Lower Peoria Lake	
	Near East Peoria	163.0–163.4
	Middle Peoria Lake	
	Near Peoria Heights Conservation Landing at Detweiller Park	169.2–171.0

Table 1.—Continued

<i>Pool</i>	<i>Station</i>	<i>River Mile^a</i>
Peoria	Chillicothe Island Chute	
	Above Chillicothe	180.1–181.0
	Henry Island Chute	
	Below Henry	193.5–194.1
	Lower Twin Sisters Island Chute	
	Above Henry	202.2–203.1
	Upper Twin Sisters Island Chute	
	Above Henry	203.1–203.5
	Hennepin Island Chute	
	At Hennepin	207.0–208.0
Starved Rock	Clark Island Chute	
	Below Spring Valley	214.9–215.6
	Bulls Island Chute	
Starved Rock	Above Ottawa	240.5–241.1
	Bulls Island Bend Section	
	Above Ottawa	241.4–241.9
Marseilles	Ballard Island Chute	
	Above Marseilles	247.8–248.2
	Johnson Island Chute	
	Above Marseilles	249.4–249.9
	Sugar Island Chute	
Dresden, Des Plaines River	Below Morris	260.2–261.0
	Rapp's Boat Yard and Du Page River Mouth	
	Above Channahon	276.8–277.8

^a Stations are located by river miles rather than by kilometers because existing river charts and navigation aids along the river use mileages.

^b Fished in 1974 but not in previous years.

Table 2.—Water temperature, dissolved oxygen and Secchi disk (S.D.) visibility values obtained during an electrofishing survey of the Illinois Waterway, 1974.

Pool	Station	River Mile	Date and Time (CST)	Water Temp. °C	D.O.*			S.D. Vis. cm
					.91 m ppm	% Sat.	Bottom ppm	
Alton	Mortland Island Chute	18.7-19.4	21 Aug-0930	27.9	6.18	80.5	6.12	18
	Diamond Island Chute	24.0-25.5	21 Aug-1520	29.5	7.31	97.3	7.09	18
	Hurricane Island Chute	26.0-27.2	22 Aug-0835	27.9	6.18	84.4	6.78	23
	Crater and Willow Island Chutes	29.3-30.7	23 Aug-0855	27.4	6.13	77.2	6.10	19
	Big Blue Island Chute	57.5-58.9	27 Aug-1430	27.5	6.18	80.5	6.02	19
La Grange	Bar and Grape Island Chutes	86.2-87.1	30 Aug-1130	25.8	5.36	67.5	5.21	20
	Sugar Creek Island Chute	94.3-95.2	16 Sep-1100	20.9	5.69	64.8	5.42	15
	Lower Bath Chute	106.8-107.5	12 Sep-1000	22.2	7.18	83.7	7.10	20
	Upper Bath Chute	112.8-113.3	12 Sep-1430	23.5	7.85	95.2	7.69	20
	Turkey Island Chute	147.3-148.2	18 Sep-1100	22.5	7.61	89.4	..	18
	Illinois River Proper	154.5-155.3	19 Sep-1345	21.3	8.21	93.2	8.20	18
Peoria	Lower Peoria Lake	163.0-163.4	29 Aug-1915	24.2	10.10	121.7	10.13	18
	Middle Peoria Lake	169.2-170.0	10 Oct-1015	13.4	8.61	82.7	8.60	22
	Chillicothe Island Chute	180.1-181.0	30 Sep-1415	16.5	6.50	68.4	5.20	17
	Henry Island Chute	193.5-194.1	1 Oct-0940	16.1	5.42	55.7	5.43	16
	Lower Twin Sisters	202.2-203.1	2 Oct-0900	16.1	6.31	64.9	6.21	17
	Upper Twin Sisters	203.1-203.5	2 Oct					
	Hennepin Island Chute	207.0-208.0	3 Oct-0920	15.5	6.51	67.0	6.49	28
	Clark Island Chute	214.9-215.6	18 Oct-0900	15.0	7.83	78.0	7.62	42
Starved Rock	Bulls Island Chute	240.5-241.1	17 Oct-0845	17.5	4.41	47.3	4.38	36
	Bulls Island Bend	241.4-241.9	17 Oct					
Marselles	Ballard Island Chute	247.8-248.2	16 Oct-1300	14.5	10.40	104.0	..	14
	Johnson Island Chute	249.4-249.9	16 Oct-0915	18.5	4.51	48.9	4.44	46
	Sugar Island Chute	260.2-261.0	15 Oct-1000	19.7	5.46	61.1	5.42	41
Dresden Pool, Des Plaines River	Du Page River Mouth	276.8-277.8	14 Oct-1245	22.0	5.09	59.3	..	32

* Method: Winkler azide (21 Aug.-19 Sept.); Oxygen analyzer (30 Sept.-18 Oct.).

Table 3.—Shortnose gar (*Lepisosteus platostomus*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00			0.00	0.00	0.00				0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.25	0.20	0.00	0.15	0.00	0.00	0.00	0.00	0.07	0.07	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.08	0.15	0.00	0.31	0.17	0.00	0.00	0.00	0.10	0.00	0.10
Alton				0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00			0.40
Ill. R. ²	0.10	0.08	0.00	0.07	0.04	0.00	0.15	0.05	0.02	0.02	0.00	#		0.12
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00			0.00	0.00	0.00				0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.20	0.17	0.00	0.12	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.03	0.13	0.00	0.09	0.04	0.00	0.00	0.00	0.10	0.00	0.09
Alton				0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00			0.07
Ill. R. ²	0.08	0.07	0.00	0.05	0.04	0.00	0.04	0.01	#	#	0.00	0.03	0.00	0.04

Table 4.—Bowfin (*Amia calva*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													
	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.04	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.10	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00			0.50
Ill. R. ²	0.00	0.00	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.05	0.00	#	0.00	0.01
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.05	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.39	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00			0.39
Ill. R. ²	0.00	0.00	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.12	0.00	0.01

Table 5.—Gizzard shad (*Dorosoma cepedianum*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
Number Per 30 Minutes														
Dresden ¹	0.00			0.00		14.16	13.83	20.83	22.17	7.49	20.50	24.70	3.33	7.30
Marseilles	2.50	4.67	5.50	7.29		13.00	2.75	13.67	13.00	12.00	15.00	0.30	4.60	13.00
Starved Rock	1.50	1.60	4.00	8.60		24.00	103.73	81.21	69.20	43.59	74.00	11.40	10.67	9.00
Peoria	21.63	45.90	26.00	218.63	59.12	92.31	29.25	23.50	35.25	38.92	22.33	47.60	21.87	16.20
La Grange	137.75	9.00		99.00	62.93	41.23	2.27	14.25	29.50	4.12	6.13		10.00	9.40
Alton				34.10	25.00	40.88								6.60
Ill. R. ²	37.00	21.76	19.70	103.62	44.71	53.62	41.21	39.51	42.48	28.07	36.25	29.90	14.25	11.26
Kilograms Per 30 Minutes														
Dresden ¹	0.00			0.00		0.61	0.02	0.37	0.73	0.29	0.46	0.76	0.08	0.05
Marseilles	0.35	0.64	0.86	0.07	0.68	1.11	0.05	0.05	0.42	0.84	0.35	0.09	0.18	0.94
Starved Rock	0.37	0.32	0.47	0.26	0.68	0.31	0.63	0.66	0.27	0.25	0.25	0.43	0.23	0.33
Peoria	1.02	3.27	1.02	1.08	2.18	0.31	1.20	0.90	1.05	1.03	1.22	0.40	0.49	0.80
La Grange	1.44	0.32		0.92	1.59	0.24	1.20	0.90	1.05	1.03	1.22	0.40	0.49	0.69
Alton				0.85	0.34	0.44	0.09	0.49	0.33	0.10	#			0.25
Ill. R. ²	0.84	1.54	0.93	0.74	1.37	0.38	0.58	0.61	0.56	0.48	0.50	0.46	0.43	0.62

Table 6.—Goldeye (*Hiodon alosoides*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
<i>Number Per 30 Minutes</i>														
Dresden ¹	0.00													
Marseilles	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40
Peoria	0.00	0.10	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.07	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.08	0.00
Alton				0.00	0.13	1.13	0.64	0.00	1.50	0.00	0.25			0.00
Ill. R. ²	0.00	0.04	0.00	0.02	0.02	0.19	0.17	0.00	0.27	0.02	0.05	#	0.03	0.05
<i>Kilograms Per 30 Minutes</i>														
Dresden ¹	0.00													
Marseilles	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Peoria	0.00	0.01	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		#	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00
Alton				0.00	#	0.05	0.07	0.00	0.07	0.00	0.01			0.00
Ill. R. ²	0.00	#	0.00	#	#	0.01	0.02	0.00	0.01	#	#	#	0.01	#

Table 7.—Mooneye (*Hiodon tergisus*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00				0.00	0.00
Marselles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
La Grange	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alton				0.00	0.12	0.00	0.36	0.00	0.00	0.00	0.00			0.00
Ill. R. ²	0.00	0.00	0.00	0.00	0.02	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00				0.00	0.00
Marselles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	#
La Grange	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alton				0.00	0.05	0.00	0.03	0.00	0.00	0.00	0.00			0.00
Ill. R. ²	0.00	0.00	0.00	0.00	0.01	0.00	#	0.00	0.00	0.00	0.00	0.00	0.00	#

Table 8.—Goldfish (*Carassius auratus*) taken by electrofishing in the Illinois Waterway, 1959–1974.

	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
<i>Pool</i>	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	<i>Number Per 30 Minutes</i>													
Dresden ¹	16.50			101.25									34.67	18.60
Marselles	18.00	34.33	33.75	12.64	19.50	7.00	9.50	6.66	7.16	3.83	6.33	6.50	0.40	2.70
Starved Rock	2.50	24.40	64.50	30.50	17.75	16.75	32.75	6.33	6.33	10.67	7.00	15.40	3.33	0.00
Peoria	0.37	0.60	3.07	0.15	0.00	2.56	1.07	0.50	0.33	0.13	1.07	0.20	0.13	0.10
La Grange	0.00	0.14		0.42	1.16	0.62	1.81	0.25	0.08	0.00	0.17	0.10	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00
Ill. R. ²	4.25	9.28	15.35	5.84	4.32	3.36	4.48	1.61	1.55	1.30	1.75	3.30	0.39	0.14
	<i>Kilograms Per 30 Minutes</i>													
Dresden ¹	2.37			..									4.53	2.27
Marselles	3.21	6.09	5.72	2.48	3.51	1.17	1.59	1.14	1.51	0.24	1.16	1.32	0.10	0.20
Starved Rock	0.34	2.76	6.71	4.50	2.88	1.99	4.18	1.07	1.18	2.09	1.40	3.28	0.89	0.00
Peoria	0.05	0.07	0.16	0.01	0.00	0.07	0.06	0.03	0.01	0.01	0.05	0.02	0.01	0.10
La Grange	0.00	0.02		0.03	0.05	0.10	0.25	0.06	#	0.00	0.01	0.02	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00
Ill. R. ²	0.73	1.32	1.92	0.95	0.71	0.37	0.60	0.26	0.29	0.18	0.27	0.68	0.10	0.05

Table 9.—Carp x Goldfish (*Cyprinus carpio* x *Carassius auratus*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													1973	1974
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971		
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	19.5	21.8
	Number Per 30 Minutes														
Dresden ¹	2.50			1.00		0.83	0.83	0.50	0.16	0.33	0.33	0.50	0.00	0.00	0.70
Marseilles	2.50	0.67	0.75	2.79	1.00	1.25	4.75	1.67	3.33	1.67	1.00	1.30	0.67	0.70	0.00
Starved Rock	0.75	4.00	0.50	3.50	3.25	1.12	1.53	2.71	2.27	1.60	1.67	2.60	1.60	1.60	1.60
Peoria	0.00	0.40	0.71	0.81	0.81	0.62	0.25	0.34	0.25	0.00	0.17	0.00	0.00	0.30	0.30
La Grange	0.25	0.00		0.04	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.70	1.04	0.70	1.14	0.73	0.77	0.98	1.16	1.09	0.70	0.73	1.20	0.72	0.72	0.64
	Kilograms Per 30 Minutes														
Dresden ¹	0.78			..		0.99	0.54	0.25	0.05	0.86	0.21	0.17	0.00	0.00	0.26
Marseilles	1.30	0.19	0.27	1.75	0.82	0.82	3.11	0.80	2.20	1.12	0.63	0.69	0.36	0.40	0.00
Starved Rock	0.73	4.05	0.57	2.05	1.75	0.27	0.43	0.78	0.63	0.42	0.46	0.80	0.39	0.33	0.33
Peoria	0.00	0.18	0.18	0.29	0.20	0.12	0.07	0.08	0.08	0.00	0.05	0.00	0.00	0.05	0.05
La Grange	0.13	0.00		#	#	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.44	0.91	0.24	0.62	0.32	0.32	0.45	0.37	0.40	0.34	0.24	0.41	0.19	0.19	0.15

Table 10.—Carp (*Cyprinus carpio*) taken by electrofishing in the Illinois Waterway, 1959-1974.

	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
<i>Pool</i>	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	<i>Number Per 30 Minutes</i>													
Dresden ¹	8.00			18.25									6.00	16.00
Marseilles	10.00	5.33	20.25	9.07	19.33	15.17	21.00	12.00	19.50	13.17	10.00	16.70	14.80	13.80
Starved Rock	3.00	28.60	53.00	25.00	26.75	11.00	31.50	19.67	15.33	9.00	9.67	18.00	4.00	10.30
Peoria	13.25	11.20	36.00	17.70	17.56	18.81	14.53	19.72	18.13	17.73	20.60	18.20	10.60	27.40
La Grange	15.00	20.71		28.42	51.69	77.39	14.63	61.75	37.59	38.91	27.58	21.60	25.23	30.50
Alton				10.70	24.50	36.63	12.55	21.87	20.88	16.00	19.50			15.70
Ill. R. ²	10.90	16.64	34.55	19.34	29.19	36.92	16.19	30.77	23.93	21.98	20.11	18.90	15.92	22.74
	<i>Kilograms Per 30 Minutes</i>													
Dresden ¹	6.36			..									4.06	7.05
Marseilles	7.53	4.45	12.40	6.67	13.34	12.53	16.70	11.55	16.51	9.91	7.91	14.91	8.66	8.76
Starved Rock	2.09	17.25	12.99	20.12	17.71	4.70	11.84	6.10	9.24	5.98	5.67	7.70	3.15	4.90
Peoria	6.81	6.70	10.26	8.18	8.00	5.79	5.72	6.90	7.78	7.22	10.17	14.13	4.84	9.78
La Grange	7.72	14.73		18.63	29.46	37.51	7.73	23.60	15.62	15.83	12.34	12.91	14.91	15.23
Alton				9.82	26.90	41.87	11.19	20.73	18.19	12.90	16.18			13.28
Ill. R. ²	6.19	10.79	10.96	12.48	18.66	21.47	9.23	14.73	12.98	10.89	11.24	13.23	8.87	11.58

Table 11.—River carsucker (*Carpodius carpio*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
Number Per 30 Minutes														
Dresden ¹	0.00			0.00			0.00	0.00	0.17	0.00	0.00		0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.00	0.00	1.00	2.40
Starved Rock	0.00	0.60	0.00	0.10	0.00	0.00	0.00	0.07	0.67	0.40	0.13	0.10	0.73	1.30
Peoria	0.12	0.70	1.71	0.19	0.00	0.00	0.07	0.07	0.67	0.40	0.13	0.10	0.73	1.30
La Grange	0.75	0.43		0.08	0.15	0.15	0.81	0.00	1.17	1.08	0.09	0.00	0.31	0.10
Alton				0.30	0.25	0.00	0.64	0.62	0.12	0.50	0.00		0.00	0.00
Ill. R. ²	0.20	0.52	1.20	0.13	0.09	0.04	0.40	0.16	0.59	0.55	0.07	0.01	0.50	0.67
Kilograms Per 30 Minutes														
Dresden ¹	0.00			0.00			0.00	0.00	0.05	0.00	0.00		0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.22	0.00	0.00	0.43	0.88
Starved Rock	0.00	0.17	0.00	0.05	0.00	0.00	0.00	#	0.21	0.14	0.10	0.06	0.21	0.31
Peoria	0.05	0.15	0.14	0.05	0.00	0.00	0.01		0.21	0.14	0.10	0.06	0.21	0.31
La Grange	0.43	0.03		0.02	0.09	0.04	0.23	0.00	0.22	0.25	0.05	0.00	0.15	0.02
Alton				0.07	0.10	0.00	0.21	0.27	0.02	0.19	0.00		0.00	0.00
Ill. R. ²	0.11	0.10	0.10	0.04	0.04	0.01	0.12	0.06	0.15	0.16	0.05	0.02	0.18	0.20

Table 13.—Smallmouth buffalo (*Ictiobus bubalus*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													
	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.10	0.20	0.00
Starved Rock	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.30	0.33	2.00
Peoria	0.13	0.20	0.36	0.56	0.75	1.87	0.13	0.79	1.47	1.20	0.60	0.20	0.40	0.70
La Grange	5.25	0.00		1.54	2.31	0.62	0.25	0.25	0.83	0.17	1.34	0.60	0.08	0.30
Alton				0.60	0.13	0.00	0.00	0.00	0.12	0.00	0.12			0.00
Ill. R. ²	1.10	0.20	0.25	0.68	0.91	0.81	0.12	0.33	0.80	0.45	0.59	0.30	0.25	0.45
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.00
Starved Rock	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.14	0.42	1.10
Peoria	0.10	0.04	0.29	0.34	0.52	1.03	0.14	0.35	0.54	0.45	0.31	0.10	0.21	0.33
La Grange	1.66	0.00		0.73	2.20	0.38	0.18	0.09	0.21	0.05	0.57	0.38	0.02	0.24
Alton				0.13	0.03	0.00	0.00	0.00	0.04	0.00	0.10			0.00
Ill. R. ²	0.37	0.15	0.20	0.33	0.79	0.45	0.10	0.14	0.26	0.17	0.28	0.16	0.13	0.25

Table 14.—Bismouth buffalo (*Ictiobus cyprinellus*) taken by electrofishing in the Illinois Waterway, 1959-1974.

	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
<i>Pool</i>	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	<i>Number Per 30 Minutes</i>													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.30
Peoria	2.25	0.70	2.57	3.89	4.56	5.12	5.00	9.22	12.20	6.87	6.20	0.90	4.33	17.20
La Grange	9.75	3.29		5.21	9.54	8.92	1.44	3.33	5.25	1.33	0.83	0.40	1.92	3.50
Alton				0.60	0.50	0.62	0.00	0.37	0.63	0.13	0.12			0.00
Ill. R. ²	2.85	1.20	1.80	2.78	4.28	4.32	1.88	4.03	5.70	2.73	2.36	0.50	2.50	6.48
	<i>Kilograms Per 30 Minutes</i>													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.12
Peoria	1.02	0.73	3.67	4.98	5.96	6.08	6.18	9.97	13.11	8.36	8.11	1.18	2.30	8.15
La Grange	10.12	4.77		4.27	8.24	8.67	1.81	3.68	6.98	1.43	1.17	0.68	1.14	1.74
Alton				0.47	0.71	0.86	0.00	1.01	0.78	0.14	0.33			0.00
Ill. R. ²	2.43	1.62	2.57	2.84	4.43	4.61	2.34	4.47	6.66	3.27	3.14	0.64	1.37	3.09

Table 16.—Shorthead redhorse (*Moxostoma macrolepidotum*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished														1973	1974
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972		
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8		
<i>Number Per 30 Minutes</i>																
Dresden ¹	..			0.00												
Marseilles	0.00	0.00	0.00	0.07	0.17	0.00	0.16	0.17	0.17	0.00	0.00	0.00	0.33	0.70		
Starved Rock	0.00	0.80	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.57	0.00		
Peoria	0.13	0.10	0.07	0.11	0.06	0.13	0.07	0.00	0.00	0.00	0.07	0.10	0.33	0.10		
La Grange	0.75	0.29		0.04	0.00	0.08	0.44	0.17	0.00	0.08	0.08	0.40	0.15	0.30		
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00			0.60		
Ill. R. ²	0.20	0.28	0.05	0.08	0.04	0.07	0.17	0.07	0.02	0.04	0.05	0.20	0.25	0.26		
<i>Kilograms Per 30 Minutes</i>																
Dresden ¹	0.05			0.00												
Marseilles	0.00	0.00	0.00	0.01	0.01	0.00	0.04	#	0.04	0.00	0.00	0.00	0.05	0.15		
Starved Rock	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.23	0.00		
Peoria	0.10	0.02	0.03	0.03	#	0.02	0.01	0.00	0.00	0.00	#	#	0.05	0.03		
La Grange	0.05	0.01		0.00	0.00	#	0.05	0.03	0.00	#	0.01	0.02	0.06	0.05		
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00			0.23		
Ill. R. ²	0.05	0.04	0.02	0.01	#	0.01	0.02	0.01	#	#	#	0.02	0.06	0.08		

Table 17.—Black bullhead (*Ictalurus melas*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.50	2.00	2.00	1.36	2.17	2.17	4.67	4.33	3.50	6.50	2.50	3.50	6.60	19.60
Starved Rock	0.00	0.60	2.00	0.20	0.00	0.00	2.25	0.00	0.33	0.00	0.00	0.00	0.00	0.00
Peoria	0.13	1.00	1.21	1.00	0.56	0.12	0.13	0.22	0.13	0.00	0.06	0.10	0.07	0.10
La Grange	0.00	0.00		0.00	0.08	0.00	0.19	0.75	0.42	0.08	0.08	0.00	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.15	0.76	1.45	0.56	0.49	0.32	0.81	0.88	0.66	0.91	0.39	0.80	0.94	2.12
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.14	0.31	0.29	0.12	0.15	0.06	0.24	0.18	0.16	0.35	0.20	0.37	0.35	0.53
Starved Rock	0.00	0.11	0.14	0.03	0.00	0.00	0.22	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Peoria	0.04	0.15	0.21	0.12	0.05	#	#	0.03	#	0.00	0.01	0.02	0.01	0.01
La Grange	0.00	0.00		0.00	#	0.00	0.01	0.01	0.04	#	#	0.00	0.00	0.00
Alton				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.04	0.12	0.22	0.06	0.04	0.01	0.05	0.04	0.04	0.05	0.03	0.09	0.06	0.06

Table 18.—Yellow bullhead (*Ictalurus natalis*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
<i>Number Per 30 Minutes</i>														
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00			0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.15	0.06	0.06	0.07	0.21	0.07	0.07	0.13	0.00	0.07	0.10
La Grange	0.00	0.72		0.04	0.08	0.15	0.00	0.08	0.08	0.00	0.08	0.00	0.00	0.10
Alton				0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.00	0.20	0.00	0.06	0.04	0.08	0.02	0.09	0.05	0.02	0.07	0.00	0.03	0.07
<i>Kilograms Per 30 Minutes</i>														
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00			0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.02	0.01	0.01	0.02	0.07	#	0.01	0.01	0.00	0.02	0.03
La Grange	0.00	0.09		0.01	0.01	0.03	0.00	#	0.02	0.00	0.01	0.00	0.00	0.03
Alton				0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ill. R. ²	0.00	0.02	0.00	0.01	#	0.01	#	0.02	#	#	0.01	0.00	0.01	0.02

Table 19.—Channel catfish (*Ictalurus punctatus*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
Starved Rock	0.00	0.20	0.00	0.70	0.00	0.00	1.25	0.33	0.00	0.00	0.00	0.30	2.00	0.00
Peoria	0.00	0.20	0.14	0.19	0.00	0.00	0.13	0.07	0.13	0.20	0.47	0.00	0.40	0.40
La Grange	0.00	4.00		1.46	2.69	0.31	0.25	2.67	2.42	2.51	1.42	1.10	0.62	1.30
Alton				3.50	8.50	2.37	2.00	3.00	1.63	4.75	2.75			5.30
Ill. R. ²	0.00	1.24	0.10	0.96	2.19	0.51	0.64	1.35	1.00	1.62	1.05	0.40	0.56	1.74
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Starved Rock	0.00	0.05	0.00	0.34	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.66	0.00
Peoria	0.00	0.03	0.02	0.07	0.00	0.00	0.01	0.01	0.04	0.05	0.31	0.00	0.21	0.19
La Grange	0.00	0.57		0.35	0.79	0.12	0.07	0.28	0.42	0.45	0.25	0.44	0.46	0.44
Alton				0.88	2.13	1.01	0.25	1.47	0.68	0.84	0.90			1.91
Ill. R. ²	0.00	0.18	0.01	0.26	0.58	0.20	0.09	0.35	0.24	0.29	0.34	0.13	0.31	0.65

Table 20.—Flathead catfish (*Pylodictis olivaris*) taken by electrofishing in the Illinois Waterway, 1959–1974.

	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
<i>Pool</i>	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	<i>Number Per 30 Minutes</i>													
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marselles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.08	0.60
Alton				0.30	0.13	0.00	0.00	0.00	0.25	0.25	0.25	0.10	0.03	0.50
Ill. R. ²	0.00	0.00	0.00	0.04	0.06	0.00	0.00	0.00	0.05	0.05	0.05	0.10	0.03	0.29
	<i>Kilograms Per 30 Minutes</i>													
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marselles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Peoria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
La Grange	0.00	0.00		0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	1.42	0.05	1.08
Alton				0.04	0.01	0.00	0.00	0.00	0.01	0.06	0.02	0.42	0.02	0.10
Ill. R. ²	0.00	0.00	0.00	#	0.06	0.00	0.00	0.00	#	0.01	#	0.42	0.02	0.31

Table 21.—White bass (*Morone chrysops*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Year and Number of Hours Fished														
Pool	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
Number Per 30 Minutes														
Dresden ¹	0.00			0.00										
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Starved Rock	0.00	0.20	0.00	0.20	0.00	0.00	0.75	1.00	0.33	0.00	0.00	0.20	0.20	0.40
Peoria	0.00	0.10	0.00	0.44	0.00	0.25	1.26	0.93	0.66	0.40	0.47	1.70	1.33	0.60
La Grange	0.00	0.29		0.33	0.46	0.15	0.94	0.75	0.58	0.25	0.00	1.30	0.93	2.20
Alton	0.00			4.40	2.62	1.62	1.27	1.00	2.00	3.49	5.75	0.80	0.08	0.80
Ill. R. ²	0.00	0.16	0.00	0.78	0.58	0.40	1.00	0.77	0.77	0.84	1.20	0.60	0.56	1.41
Kilograms Per 30 Minutes														
Dresden ¹	0.00			0.00										
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	#	0.00	0.00	0.00	0.00	#	0.00	0.00
Starved Rock	0.00	#	0.00	0.06	0.00	0.00	0.07	0.21	0.10	0.00	0.00	0.07	0.01	0.09
Peoria	0.00	0.02	0.00	0.10	0.00	0.07	0.15	0.26	0.27	0.19	0.00	0.16	0.06	0.08
La Grange	0.00	0.13		0.09	0.06	0.00	0.15	0.20	0.20	0.10	0.12	0.27	0.05	0.21
Alton	0.00			1.03	0.80	0.26	0.25	0.14	0.62	1.28	1.14	0.27	#	0.12
Ill. R. ²	0.00	0.05	0.00	0.18	0.15	0.07	0.15	0.18	0.27	0.32	0.25	0.15	0.04	0.50
														0.23

Table 23.—Bluegill (*Lepomis macrochirus*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.25	1.00	0.00	0.14	0.17	0.00	0.00	0.00	0.00	0.17	0.00	2.00	0.00	0.90
Starved Rock	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00
Peoria	1.75	0.20	3.93	3.07	7.31	5.06	0.20	3.14	1.80	1.80	1.80	1.90	2.20	9.30
La Grange	0.25	24.71		11.13	7.54	6.92	0.06	3.34	3.08	5.09	3.08	7.90	4.92	14.60
Alton				4.30	3.50	5.13	0.00	4.38	3.12	3.75	7.25			12.70
Ill. R. ²	0.80	7.16	2.75	4.65	5.19	4.51	0.08	2.77	2.02	2.70	2.82	3.50	2.69	9.93
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	#	0.04	0.00	#	#	0.00	0.00	0.00	0.00	#	0.00	0.03	0.00	0.04
Starved Rock	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Peoria	0.08	#	0.23	0.11	0.05	0.03	#	0.02	0.01	#	0.03	0.05	0.04	0.18
La Grange		0.89		0.30	0.06	0.04	#	0.10	0.07	0.18	0.07	0.20	0.12	0.51
Alton	#			0.12	0.01	0.01	#	0.05	0.12	0.16	0.37			0.50
Ill. R. ²	0.04	0.26	0.16	0.13	0.04	0.02	#	0.05	0.05	0.08	0.10	0.09	0.06	0.31

Table 24.—Largemouth bass (*Micropterus salmoides*) taken by electrofishing in the Illinois Waterway, 1959-1974.

Pool	Year and Number of Hours Fished														
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974	
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8	
Number Per 30 Minutes															
Dresden ¹	0.00			0.00									0.00	0.00	
Marseilles	0.00	0.67	0.50	0.07	0.00	0.17	0.00	0.17	0.00	0.17	0.50	0.10	2.40	1.78	
Starved Rock	0.00	0.60	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	1.00	0.00	
Peoria	2.13	3.20	10.36	4.85	2.69	1.13	0.27	0.21	0.87	0.67	0.27	0.80	6.20	5.78	
La Grange	8.00	20.71		8.71	2.15	2.15	0.06	0.92	1.17	1.42	1.25	2.50	3.38	2.55	
Alton				3.70	0.62	0.63	0.00	1.13	2.50	0.63	1.75			4.30	
Ill. R. ²	2.45	7.28	7.35	4.45	1.62	1.11	0.12	0.56	1.07	0.75	0.82	1.10	4.19	3.74	
Kilograms Per 30 Minutes															
Dresden ¹	0.00			0.00									0.00	0.00	
Marseilles	0.00	0.04	0.01	#	0.00	0.01	0.00	0.01	0.00	0.00	0.08	#	0.76	0.15	
Starved Rock	0.00	0.23	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.21	0.00	
Peoria	0.80	0.98	2.32	1.83	0.90	0.36	0.15	0.07	0.15	0.14	0.04	0.22	1.41	1.57	
La Grange	2.06	5.11		2.74	0.73	0.64	0.01	0.27	0.33	0.37	0.14	0.31	0.72	0.92	
Alton				1.11	0.29	0.12	0.00	0.22	0.64	0.10	0.53			0.94	
Ill. R. ²	0.73	1.87	1.63	1.49	0.56	0.32	0.05	0.14	0.25	0.16	0.16	0.18	0.97	0.99	

Table 25.—White crappie (*Pomoxis annularis*) taken by electrofishing in the Illinois Waterway, 1959–1974.

<i>Pool</i>	<i>Year and Number of Hours Fished</i>															
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974		
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8		
	<i>Number Per 30 Minutes</i>															
Dresden ¹	0.00			0.00		0.00	0.00	0.33	0.00	0.00	0.00	0.50	0.00	0.00		
Marseilles	0.00	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Starved Rock	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30
Peoria	0.25	0.00	1.36	1.41	1.31	0.63	0.20	2.64	1.80	0.33	0.47	1.30	3.33	5.50	0.00	0.30
La Grange	0.00	4.29		3.63	0.62	1.00	0.13	2.08	3.17	3.08	1.25	1.50	0.46	1.50	0.00	1.50
Alton				0.50	0.88	0.88	0.64	1.00	1.37	1.99	1.63			0.70	0.00	0.70
Ill. R. ²	0.10	1.48	0.95	1.53	0.77	0.64	0.23	1.68	1.73	1.32	0.80	1.00	1.56	2.57		2.57
	<i>Kilograms Per 30 Minutes</i>															
Dresden ¹	0.00			0.00		0.00	0.00	0.06	0.00	0.00	0.00	0.06	0.00	0.00		0.00
Marseilles	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
Starved Rock	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Peoria	0.01	0.00	0.15	0.17	0.18	0.11	0.00	0.39	0.28	0.08	0.07	0.21	0.50	1.02	0.00	1.02
La Grange	0.00	0.33		0.31	0.09	0.15	0.03	0.20	0.42	0.47	0.13	0.23	0.05	0.13	0.00	0.13
Alton				0.10	0.10	0.13	0.08	0.27	0.25	0.34	0.22			0.19	0.00	0.19
Ill. R. ²	#	0.11	0.11	0.15	0.10	0.10	0.03	0.24	0.25	0.22	0.10	0.16	0.23	0.44		0.44

Table 26.—Black crappie (*Pomoxis nigromaculatus*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1973	1974
	12.0	12.5	10.0	44.5	23.5	23.5	26.0	21.5	22.0	22.0	22.0	13.5	19.5	21.8
Number Per 30 Minutes														
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00	0.17	0.10	0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.40
Starved Rock	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.40
Peoria	0.00	0.00	2.36	7.56	1.75	0.56	0.00	1.64	2.33	1.34	1.53	2.60	4.47	8.00
La Grange	0.75	8.71		5.67	1.15	1.85	0.44	5.00	8.00	11.50	8.42	6.90	4.23	9.50
Alton				0.00	2.50	1.50	0.45	1.75	3.63	6.88	8.38			1.80
Ill. R. ²	0.20	2.44	1.65	4.30	1.34	0.96	0.23	2.26	3.64	4.85	4.36	3.00	3.47	5.62
Kilograms Per 30 Minutes														
Dresden ¹	0.00			0.00		0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Marseilles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Starved Rock	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.33
Peoria	0.00	0.00	0.30	1.58	0.29	0.10	0.00	0.24	0.53	0.25	0.31	0.48	0.52	1.37
La Grange	0.08	1.16		1.08	0.12	0.09	0.07	0.50	0.97	1.38	0.82	0.91	0.56	0.74
Alton				0.34	0.25	0.25	0.03	0.24	0.26	0.90	1.48			0.23
Ill. R. ²	0.01	0.33	0.21	0.85	0.17	0.10	0.03	0.26	0.49	0.63	0.60	0.44	0.43	0.72

Table 27.—Freshwater drum (*Aplodinotus grunniens*) taken by electrofishing in the Illinois Waterway, 1959–1974.

Pool	Year and Number of Hours Fished													
	1959 12.0	1960 12.5	1961 10.0	1962 44.5	1963 23.5	1964 23.5	1965 26.0	1966 21.5	1967 22.0	1968 22.0	1969 22.0	1970 13.5	1973 19.5	1974 21.8
	Number Per 30 Minutes													
Dresden ¹	0.00			0.00									0.00	0.00
Marseilles	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.50	0.33	0.70	0.00	0.40
Starved Rock	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00
Peoria	0.38	0.10	0.79	0.40	0.06	0.31	0.07	0.00	0.13	0.20	0.53	0.50	0.73	0.60
La Grange	3.25	2.00		0.92	0.69	0.54	1.56	1.33	3.50	2.75	3.92	2.30	4.62	5.00
Alton				0.30	0.87	0.00	3.55	0.38	0.38	1.12	1.12	1.00	1.97	5.70
III. R. ²	0.80	0.60	0.55	0.45	0.36	0.26	1.25	0.44	1.07	1.09	1.52	1.00	1.97	2.90
	Kilograms Per 30 Minutes													
Dresden ¹	0.00			0.00								#	0.00	0.00
Marseilles	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	#
Starved Rock	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Peoria	0.03	#	0.09	0.06	0.03	0.15	#	0.00	#	0.05	0.18	0.10	0.01	0.03
La Grange	0.33	0.38		0.10	0.11	0.05	0.24	0.14	0.25	0.24	0.62	0.29	0.52	0.46
Alton				0.01	0.09	0.00	0.20	0.05	0.02	0.11	0.12		0.49	0.49
III. R. ²	0.08	0.11	0.06	0.06	0.06	0.06	0.12	0.05	0.07	0.10	0.26	0.12	0.19	0.24

Table 28.—Summary of the commercial catch of fish from the Illinois Waterway and the Mississippi River bordering Illinois, 1950-1973.*

Species	1950	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
	Thousand Kilograms																				
Bowfin	5	2	1	1	1	3	3	1	3	3	b	1	b	b	b	b	1	b	b	b	b
Buffalo	622	567	469	365	464	400	486	378	418	344	447	298	279	327	428	385	378	241	209	118	54
Carp	1833	808	1074	851	626	723	596	524	486	537	486	337	330	354	355	246	397	188	342	142	97
Catfish & bullheads	88	85	136	141	106	94	72	74	62	74	60	59	37	40	45	44	67	43	30	28	28
Garfish	..	..	..	..	b	1	..	..	b	..	b	3	1	1	..	2	b	b	..	..	..
Paddlefish	12	1	4	3	b	2	..	..	b	b	b	..	..	4	1	b	3	3	..	2	b
Quillback	..	2	78	..	..	1	3	3	..	..	..	1	..	..	1	3	..	b	..	..	..
Sheepshead (shovelnose)	52	90	44	82	56	63	24	31	21	27	18	18	10	10	17	9	20	12	20	8	3
Sturgeon	b	1	..	..	b	..	..	..	..	..	..	..	..	..	..	..	..	b	..	..	b
Suckers	1	b	1	b	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
Yellow bass	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Crappie	..	..	11	16	12	15	13	11	14	15	2	..	..	..	..	..	..	..	..	..	..
Carp sucker	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	b
Yellow perch	..	b	1	..	b	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
White bass	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Total fish, Ill. River	2613	1556	1816	1460	1266	1302	1197	1025	1005	1000	1016	717	657	737	848	690	866	487	602	297	182
No. of Ill. River fishermen																					
Full time	106	..	..	..	..	..	..	69	..	..	..	..	..	..	..	..	..	22	9	13	13
Part time	169	..	..	..	..	..	..	73	..	..	..	..	..	..	..	..	..	46	47	42	56
Total fish,																					
Miss. R. bordering Ill.	1326	1236	1766	1501	1462	1909	1973	1916	1440	1571	1664	1469	1574	1567	1317	1211	1310	1442	1379	1473	1637

* Most of the statistics were obtained from statistical digests published by the U.S. Dept. of Commerce. The 1972 and 1973 data and the number of full time and part time commercial fishermen on the Illinois River were provided by Mr. Larry Dunham, Fisheries Biologist, Illinois Department of Conservation.

b Less than 1000 kg.

Table 29.—Average number of kilograms of fish taken per 30 minutes of electrofishing in each navigation pool of the Illinois Waterway during the period 1959–1974.

Ref. Table No.	Species	Pools					
		Downstream			Upstream		
		Alton	La Grange	Peoria	Starved Rock	Mar- seilles	Dres- den
3	Shortnose gar	0.01	0.04 ^a	0.04 ^a	0.00	0.00	0.00
4	Bowfin	0.05 ^a	0.05	0.01	0.00	0.00	0.00
5	Gizzard shad	0.36	0.88	0.90 ^a	0.40	0.47	0.03
6	Goldeye	0.02 ^a	#	#	0.00	#	0.00
7	Mooneye	0.01 ^a	0.00	#	0.00	0.00	0.00
8	Goldfish	0.00	0.04	0.05	2.38	2.10	3.05 ^a
9	Carp x goldfish	#	0.05	0.38	1.37 ^a	0.53	0.35
10	Carp	19.01 ^a	17.40	8.02	9.24	10.85	5.82
11	River carpsucker	0.10	0.12	0.10	0.14 ^a	0.02	0.00
12	Quillback carpsucker	0.03	0.03	0.14	0.50 ^a	0.20	0.00
13	Smallmouth buffalo	0.03	0.52 ^a	0.34	0.17	#	0.00
14	Bigmouth buffalo	0.48	4.21	5.70 ^a	0.02	#	0.00
15	Black buffalo	0.06	0.25 ^a	0.20	0.01	0.00	0.00
16	Shorthead redhorse	0.03	0.02	0.02	0.04	0.01	0.06 ^a
17	Black bullhead	0.00	#	0.05	0.04	0.24 ^a	0.00
18	Yellow bullhead	#	0.01 ^a	0.01 ^a	0.00	0.00	0.00
19	Channel catfish	1.12 ^a	0.36	0.07	0.09	0.01	0.00
20	Flathead catfish	0.03	0.21 ^a	0.00	0.00	0.00	0.00
21	White bass	0.67 ^a	0.10	0.11	0.05	0.01	0.00
22	Green sunfish	0.01	0.09 ^a	0.06	0.02	0.02	#
23	Bluegill	0.15	0.20 ^a	0.06	#	0.01	0.00
24	Largemouth bass	0.44	1.11 ^a	0.78	0.04	0.08	0.00
25	White crappie	0.19	0.20	0.23 ^a	0.01	0.03	0.00
26	Black crappie	0.44	0.65 ^a	0.43	0.03	#	0.00
27	Freshwater drum	0.12	0.29 ^a	0.05	0.01	#	0.00

^a Indicates the pool or pools where the maximum number of kilograms of each species was taken in the period 1959–1974.

Less than 0.01 kilogram taken.

Table 30.—Average number of fish taken per 30 minutes of electrofishing in each navigation pool of the Illinois Waterway during the period 1959–1974.

Ref. Table No.	Species	Pools					
		Downstream			Starved Rock	Upstream	
		Alton	La Grange	Peoria		Mar- seilles	Dres- den
3	Shortnose gar	0.07 ^a	0.07 ^a	0.05	0.00	0.00	0.00
4	Bowfin	0.07 ^a	0.02	0.01	0.00	0.00	0.00
5	Gizzard shad	18.09	43.55	63.20 ^a	9.22	12.52	2.66
6	Goldeye	0.41 ^a	0.02	0.02	0.00	0.03	0.00
7	Mooneye	0.05 ^a	0.00	0.01	0.00	0.00	0.00
8	Goldfish	0.00	0.37	0.73	17.02	12.02	42.76 ^a
9	Carp x goldfish	0.01	0.18	1.39	2.02 ^a	0.80	1.05
10	Carp	19.81	34.69 ^a	18.67	18.92	14.29	12.06
11	River carpsucker	0.27	0.39	0.44 ^a	0.34	0.04	0.00
12	Quillback carpsucker	0.11	0.16	0.52	1.38 ^a	0.71	0.00
13	Smallmouth buffalo	0.11	1.04 ^a	0.67	0.25	0.03	0.00
14	Bigmouth buffalo	0.33	4.21	5.79 ^a	0.05	0.01	0.00
15	Black buffalo	0.04	0.24 ^a	0.19	0.02	0.00	0.00
16	Shorthead redhorse	0.08	0.21	0.09	0.02	0.00	0.00
17	Black bullhead	0.00	0.12	0.35	0.38	4.39 ^a	0.00
18	Yellow bullhead	0.01	0.10 ^a	0.07	0.00	0.00	0.00
19	Channel catfish	3.76 ^a	1.60	0.17	0.34	0.01	0.00
20	Flathead catfish	0.19 ^a	0.09	0.00	0.00	0.00	0.00
21	White bass	2.65 ^a	0.42	0.64	0.44	0.07	0.00
22	Green sunfish	0.52	1.77	2.91 ^a	0.65	1.01	0.23
23	Bluegill	4.90	7.12 ^a	3.10	0.06	0.33	0.00
24	Largemouth bass	1.70	4.23 ^a	2.82	0.13	0.47	0.00
25	White crappie	1.07	1.75 ^a	1.47	0.05	0.32	0.00
26	Black crappie	2.99	5.55 ^a	2.44	0.18	0.04	0.00
27	Freshwater drum	1.49	2.49 ^a	0.34	0.03	0.14	0.00

^a Indicates the pool or pools where the maximum number of individuals of each species was taken in the period 1959–1974.

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**Pesticides and
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in Illinois**

**Robert L. Metcalf
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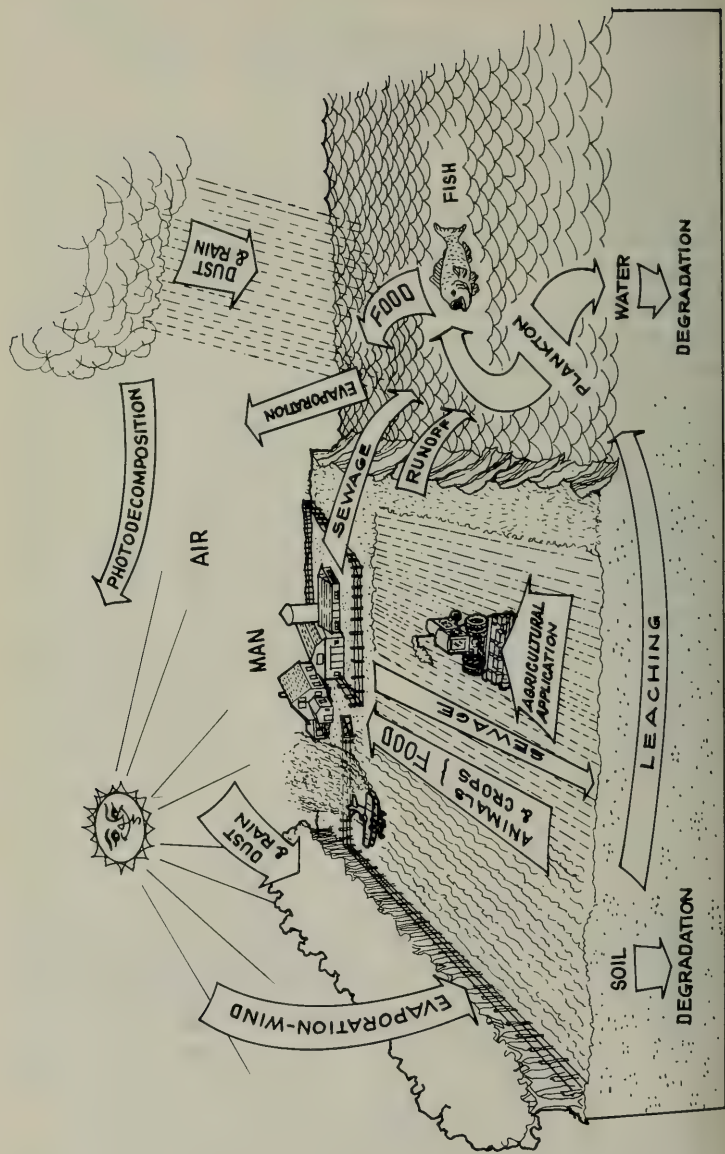
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Robert L. Metcalf is Professor of Biology and Research Professor of Entomology, University of Illinois. James R. Sanborn is an Assistant Entomologist, Illinois Natural History Survey.



Frontispiece. Ways in which pesticides move away from the target site to contaminate the total environment, entering into a variety of cycles in

Pesticides and Environmental Quality in Illinois

Robert L. Metcalf

James R. Sanborn

ILLINOIS has 29,039,000 acres (1.18×10^7 ha) of farmland, amounting to 84 percent of its land surface. This land is among the most fertile and productive in the world, and Illinois ranks as the second state, after California, in producing farm crops, valued at \$3.167 billion in 1973. Illinois land produced 996,010,000 bushels (2.53×10^{10} kg) of corn (17.6 percent of the U.S. total), 290,745,000 bushels (7.9×10^8 kg) of soybeans (18.6 percent of the U.S. total), 37,800,000 bushels (1.03×10^9 kg) of wheat (2.2 percent of the U.S. total), 19,780,000 bushels (2.88×10^8 kg) of oats (30 percent of the U.S. total), 3,251,000 tons (2.95×10^9 kg) of hay (2.4 percent of the U.S. total), and 4,225,000 pounds (1.92×10^6 kg) of red clover seed (15 percent of the U.S. total). From these plant products Illinois produced an additional \$1.906 billion worth of livestock (4.2 percent of the U.S. total) (Illinois Cooperative Crop Reporting Service 1973).

The value of Illinois farmland exceeds \$30 billion by current land value, and its corn crops alone have been valued at more than \$30 billion over the past 100 years. However, in terms of its capability to help to feed a world which is growing ever hungrier, the value of Illinois soil can scarcely be overestimated.

ACKNOWLEDGMENTS

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USE OF PESTICIDES

Modern agricultural practices—involving superior plant varieties, improved cropping methods, heavy applications of nitrogenous fertilizers, and extreme reliance on agricultural chemicals, especially herbicides and insecti-

cides—have been responsible for the state's immense agricultural productivity. These innovations have seen Illinois corn yields increase from 30 bushels per acre (1,601 kg per ha) in 1920 to 105 bushels per acre (6,605 kg per ha) in 1973. The use of pesticides in corn production has been described as being "as significant as the plow." Their use has increased phenomenally, and in Illinois more total acreage, more than 14 million acres (5.67×10^6 ha), is treated with pesticides than is treated in any other state (Fowler & Mahan 1972). In 1972 herbicides were applied to 14,326,000 acres (5.79×10^6 ha) (49 percent of Illinois farmland) and insecticides to 5,946,000 acres (2.41×10^6 ha) (20 percent of Illinois farmland) (Illinois Cooperative Crop Reporting Service 1973). On an acreage basis 14.7 percent of the herbicides and 14.1 percent of the insecticides used in U.S. agriculture were applied in Illinois although the state has only about 2.5 percent of the total cultivated land. We estimate (U.S. Environmental Protection Agency 1972a; Illinois Cooperative Crop Reporting Service 1973) that about 34 million pounds (1.54×10^6 kg) of the active ingredients of pesticides were applied to Illinois farm soil in 1971—equivalent to 1 pound for each acre (1.1 kg per ha) in the state or 3 pounds (1.36 kg) for each of the state's 11 million inhabitants.

Much of the total amount of pesticides applied is dispersed throughout the environment (Frontispiece), entering air, water, and food through volatilization and air currents, runoff and leaching, and uptake and concentration in food chains.

NEED FOR SURVEILLANCE

The heavy use of pesticides, changing agricultural technology, and the rapid introduction of new pesticide products present a continuing demand for evaluation and surveillance of the effects of pesticides upon environmental

quality. The long-term effects of widely used pesticides are not well appreciated. Thus, von Rümker and Horay (1972), after a detailed survey of the most widely used pesticides, concluded that for 20 of the 35 compounds studied there was inadequate information about the nature of the environmental degradation products and their effects on environmental quality. Considering that many of these pesticides, such as chlordane, toxaphene, dieldrin, propanil, captan, zineb, and maneb, were introduced 20 or more years ago, the magnitude of the problem is apparent. Furthermore, insect resistance to the organochlorine insecticides, together with increasingly severe effects of their use upon environmental quality, have resulted in their gradual replacement with organophosphorus and carbamate insecticides (Table 1).

New pesticides are being introduced at a rate much faster than that of our scientific appreciation of their environmental effects. During the 30 years since World War II, the number of synthetic fungicides, herbicides, insecticides, nematocides, and rodenticides has increased from less than 100 to over 900. The scene changes constantly with the development of new products and new technologies such as no-till farming. During 1974, for example, the following new pesticides were introduced under experimental permit into Illinois agriculture: cyprazine (Prefox®), metribuzin (Sencor®), bentazon (Basagran®), oryzalin (Surflan®), profluralin (Tolban®), dinitramine (Cobex®), bifenox (MODOWN®), glyphosate (Round-up®), Rowtate®, and Counter®. Pesticides introduced under such experimental permits may be used on hundreds of thousands to millions of acres of Illinois soil in a few years. Thus, carbofuran, introduced in 1968, was used to treat 706,000 acres (287,000 ha) in 1971, and trifluralin, introduced in 1964, was used to treat 1,226,000 acres (496,000 ha) in 1971 (Petty & Kuhlman 1972).

Table 1.—Use of organochlorine insecticides on Illinois farms.

Year	Insecticide Used and Acres Treated					
	aldrin	dieldrin	DDT	chlordane	heptachlor	toxaphene
1968	3,438,000 ^a	...	...	82,500	822,000	...
1969	3,512,000	11,000	9,000	160,000	1,131,000	24,000
1970	2,690,000	...	...	63,800	822,000	...
1971	1,690,000 (2,240,000)	0	0	233,000 (87,000)	232,000 (654,000)	...
1972	1,268,000 (1,883,000)	0	0	375,000	181,000	(35,000)
1973	...	...	...	...	...	...
1974	1,400,000	0	0	200,000	400,000	(100,000)

^a Data from Petty (1974) and data in parentheses from Illinois Cooperative Crop Reporting Service (1970 and 1973).

In addition, farmers are increasing their use of combinations or mixtures of pesticides, either prepackaged or in-tank mixed. This proliferation of materials and their persistence may provide unintended soil mixtures. Pesticides are, by design, highly reactive biological compounds and may interact with one another in many ways to produce unintended effects, e.g., synergism in which the combined action is far greater than that of either of the components alone. Thus, the study of pesticide interactions in relation to environmental quality is much more complicated than the study of the individual components. As an example of this complexity, 29 combinations of herbicides were registered for use on corn and soybeans in Illinois in 1974 (McGlamery et al. 1974).

BENEFIT-RISK OF PESTICIDE USE

The use of pesticides in such a prodigious way obviously poses benefit-risk questions which are very difficult to answer satisfactorily, especially in regard to the effects of pesticides on the total quality of the environment and on the long-term productivity of Illinois soil. Two examples will illustrate this point.

The use of certain preemergence herbicides allows no choice between planting corn or soybeans. The unusu-

ally wet May and June of 1974 prevented corn production in many areas on land already treated with atrazine. This herbicide is highly toxic to soybeans so that this crop was precluded as an alternative although it might have been the most profitable crop over a shortened growing season.

The soil insecticide aldrin is converted by the action of air, bacteria, and enzymes in plants and animals to the epoxide dieldrin, one of the most persistent of all pesticides. More than 60 million pounds (2.72×10^7 kg) of aldrin have been applied in Illinois since 1954, and the soil of this state has the highest average levels in the nation of aldrin (0.13 ppm) and dieldrin (0.11 ppm) (Wiersma et al. 1972). The national averages are 0.02 ppm for aldrin and 0.03 ppm for dieldrin. Soybeans grown on soil long planted in corn average about 0.01 ppm of dieldrin although they have no federal tolerance. Dieldrin residues in Illinois milk consistently exceed legal limits, and highly dieldrin-contaminated soybean sludges fed to poultry have resulted in the seizure and destruction of more than 25 million chickens in Mississippi (Anonymous 1974).

EARLY-WARNING TECHNOLOGY

The thoroughly unsatisfactory situation in Illinois, resulting from the

widespread use of highly persistent organochlorine pesticides with little or no prior understanding of their fates in the total environment, has prompted both scientific and lay concern about a screening methodology which could serve as a simple early-warning system against potentially undesirable or hazardous effects of the large-scale use of new agricultural chemicals or combinations of them. The wait-and-see system, followed in the use of aldrin, dieldrin, heptachlor, and chlordane and requiring a generation or more to distinguish serious environmental pollution, is demonstrably inadequate and has resulted in such disasters as the widespread contamination and seizure of milk supplies, the destruction of millions of contaminated chickens, and the devastation of valuable fishing industries.

A recent comprehensive study, *Pesticide Use on the Nonirrigated Croplands of the Midwest* (U.S. EPA 1972a)

recommended that "a massive, interdisciplinary research effort be mounted to clarify the environmental behavior of major pesticides which are expected to continue in use for the foreseeable future." Information needed includes the fates of pesticides in the environment after application; routes of metabolism, degradation, and disappearance; natures of the ultimate breakdown products; effects of long-term exposure of ecosystems to low-level residues; and interactions with other chemicals in the environment. It will be necessary to establish an order of priority among products to be investigated in this fashion.

The investigations reported here represent an effort by the State of Illinois, through the Illinois Natural History Survey and the University of Illinois, to assume the responsibility for the comprehensive research so urgently needed on the total environmental fates of new pesticides.

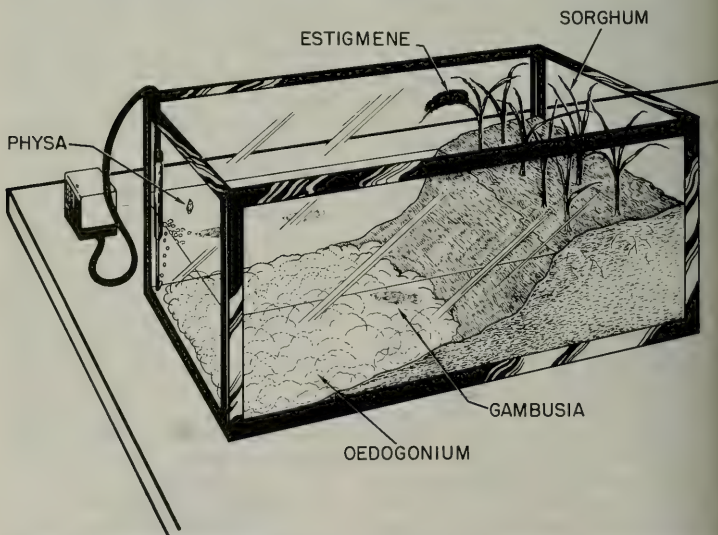


Fig. 1.—The laboratory model ecosystem used to evaluate the fates and environmental effects of radiolabeled pesticides on terrestrial and aquatic organisms, including sorghum, salt-marsh caterpillar, plankton, alga, snail, mosquito larva, and mosquito fish.

MODEL-ECOSYSTEM TECHNOLOGY

The development of model-ecosystem or microcosm technology (Metcalf et al. 1971; Metcalf 1974) has provided a quick and sensitive laboratory tool for providing answers to these questions about environmental pollution by pesticides:

1. The nature of the biological effects on non-target organisms
2. The nature of degradative pathways and the magnitudes of degradative products
3. The bioconcentration and ecological magnification (EM) of parent compounds and degradation products in living organisms
4. The quantitative estimation of persistence and biodegradability

Basically, model-ecosystem evaluation uses radiolabeled pesticides to follow qualitatively and quantitatively the movement and degradation of the compounds from a terrestrial (farm) environment into an aquatic (lake) environment and to demonstrate the passage of the parent compound and its transformation products through aquatic food webs. The experimental model is shown in Fig. 1 and consists of a 20-gallon aquarium with a sloping shelf of washed quartz sand entering a lake of 7 liters of standard reference water (Freeman 1953), which provides mineral nutrition for plankton, alga, snail, mosquito larva, and fish and for sorghum plants growing on the terrestrial farm area. The water phase of the system is aerated, and the entire system is kept in an environmental plant growth chamber at 80°F (26.5°C) with a 12-hour diurnal cycle of 5,000 foot candles of fluorescent light.

The radiolabeled pesticide to be tested is applied to sorghum plants, seeds, or to the soil of the system, using a realistic dosage of 1–5 mg per experiment, equivalent to 0.2–1.0 pound per acre (0.22–1.1 kg per ha). Ten last-instar salt-marsh caterpillars, *Estig-*

mene acraea, are introduced to consume the treated sorghum plants, and the caterpillars and their excretory products, leaf frass, etc., contaminate the lake portion of the model system. The radiolabeled products enter the various aquatic food chains, e.g., plankton → daphnia (*Daphnia magna*) → mosquito (*Culex pipiens*) → fish (*Gambusia affinis*) or alga (*Oedogonium cardiacum*) → snail (*Physa* spp.).

The movement of the radiolabeled products from plants to lake are measured by counting the radioactivity of duplicate 1-ml water samples by liquid scintillation at intervals of 1, 2, 4, 7, 14, 21, 28, and 33 days or whenever desired. After the system has been in operation for 26 days, 300 mosquito larvae are added, and after 4 more days 50 are removed for analysis. The food chains are completed after 30 days by adding three mosquito fish, *G. affinis*, which are left for 3 days to eat the daphnia and mosquito larvae.

The experiment is terminated after 33 days, when weighed samples of the various organisms are homogenized in small volumes of acetonitrile. Aliquots are counted for total radioactivity by liquid scintillation. One liter of water from the system is extracted three times with diethyl ether to measure total radioactivity. The residual water is hydrolyzed with 1.0 N hydrochloric acid for 4 hours and reextracted with diethyl ether to determine the conjugated materials, and the amount of unextractable radioactive materials is determined by counting the radioactivity of the remainder.

The acetonitrile extracts of the organisms are concentrated to a few milliliters and known volumes are applied to thin-layer chromatography (TLC) plates of fluorescent silica gel (E. Merck GF-254). TLC is carried out with appropriate solvents (identified in the tables) and with the incorporation of standard known metabolites of the pesticide under study. After the chro-

matograms are developed, they are placed against X-ray film and exposed for several weeks to several months to determine the areas containing radiolabeled products. These areas are scraped into scintillation vials, and scintillation counts are made to determine the amounts of individual degradation products present. The residues from the tissue extractions are combusted to determine the amount of unextractable radioactive materials, using either the Schoeniger oxygen flask technique (Kelly et al. 1961) or a tissue solubilization method.

After the completion of these assays, the results of the experiment are assembled on balance sheets showing the amounts and natures of radiolabeled degradation products present. Wherever possible, the chemical identities of the degradation products are determined by cochromatography with known model compounds, by the use of specific microchemical reactions and by infrared and mass spectrometry. The results of such studies on 48 pesticides are shown in the tables.

HERBICIDE TEST RESULTS

The importance of examining the fates of herbicides in a terrestrial-aquatic model ecosystem cannot be overestimated, especially in view of the exponential growth in the use of herbicides over the past 20 years in the United States. Pimental et al. (1973) estimated that in 1945 the use of herbicides for controlling weeds in corn was practically nonexistent. However, in the 25-year period from 1945 to 1970 the use of herbicides increased significantly, and it was estimated that by 1970 herbicide treatment averaged 1 pound of active ingredient per acre (1.1 kg per ha). Though figures were not available for 1945, it is possible to examine figures for 1950-1970, which clearly demonstrate that herbicide use on corn increased at least twentyfold during that time.

Alachlor, or 2-chloro-2', 6'-diethyl-N-(methoxymethyl)-acetanilide, is a member of a large class of chloro-acetanilide herbicides used to control annual grasses in cornfields and certain broadleaf weeds in corn or soybeans. The data clearly indicate the susceptibility of this herbicide to extensive degradation, as no residues of alachlor were isolated from any of the test organisms (Table 2). The high degree of degradation is further evidenced by the large number (10) of radiolabeled products of alachlor isolated from the water section of the ecosystem. Continued use of this herbicide should not lead to its accumulation in aquatic food chains.

Atrazine, or 2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine, is one of the most extensively used herbicides for controlling weeds in corn plantings. The alga, snail, and fish of the model ecosystem contained 2.4059, 0.2386, and 0.3511 ppm, respectively, of atrazine (Table 3). The percentages of atrazine in the radioactive materials extractable from the alga, snail, and fish were 87.3, 63.1, and 59.3, respectively. The EM values for atrazine for the alga, snail, and fish were 75.6, 7.5, and 11.0, respectively. In addition, the alga, snail, and fish contained smaller amounts, 0.2100, 0.05479, and 0.07356 ppm, respectively, of *N*-dethylatrazine (compound A, Table 3). Another *N*-dealkylated product, *N*-deisopropylatrazine (compound B, Table 3), was isolated from the alga (0.04934 ppm), snail (0.02796 ppm), and fish (0.05496 ppm). The EM values of these two dealkylated metabolites were of the same order of magnitude as that observed for atrazine. Continued use of atrazine would not appear to lead to major accumulations in aquatic food chains.

Bentazon, or 3-isopropyl-1*H*-2,1,3-benzothiadiazin-4-(3*H*)-one-2,2-dioxide, is a new herbicide employed for the control of a selected number of broadleaf and sedge weeds. In the

model ecosystem (Booth et al. 1973) it was susceptible to degradation, as indicated by the lack of residues in all organisms except the clam, which contained 0.622 ppm of *N*-isopropylanthranilamide, 1.266 ppm of anthranilic acid, and 0.510 ppm of unchanged bentazon (Table 4). The percentage of bentazon in the radioactive materials extractable from the clam was 18.7, and the EM value was about 10. Continued use of this herbicide should not lead to its accumulation in aquatic food chains.

Cyanazine, or 2-chloro-4-(1-cyano-1-methylethylamino)-6-ethylamino-s-triazine, is used for the control of annual grasses and broadleaf weeds in cornfields. The behavior of this herbicide in the model ecosystem indicates that it is susceptible to degradation, as only the water plant, *Elodea*, contained residues of this herbicide (Table 5). Neither the fish nor the snail contained residues of cyanazine or its degradation products. The high water solubility, 171 ppm, of cyanazine and its apparent susceptibility to degradation clearly demonstrate that the continued use of cyanazine should not result in its accumulation in aquatic food chains.

Dicamba, or 3,6-dichloro-*o*-anisic acid, is an effective herbicide for the control of both annual broadleaf weeds and grasses in corn. The data indicate clearly that this herbicide is not absorbed by the organisms of the model ecosystem (Yu et al. 1975a) (Table 6). This fact is probably related to the pH of the aqueous portion of the model ecosystem, which is higher than the pK_a (dissociation constant) of this benzoic acid derivative; therefore, the herbicide exists in the ionic form. Dicamba in the ether-extracted water constitutes about 90 percent of the extractable radioactive materials. Although the data do not indicate it, dicamba was recovered from the water only after acidification and heating for 24 hours. It is impossible to state whether the dicamba was in the ionic form and that acidification facilitated

the partition of dicamba into ether, or whether the dicamba was present as a conjugate and that the acid treatment broke down the conjugate and released the free acid. In any case, very little happened to dicamba in the water of the model ecosystem other than conjugation through the carbonyl moiety.

Phenmedipham, or methyl *m*-hydroxycarbanilate *m*-methylcarbanilate, is a postemergence herbicide used in sugar beets to control a large variety of annual weeds. The fate of phenmedipham in this model ecosystem clearly indicates the susceptibility to degradation of this herbicide, as none of the organisms contained phenmedipham residues (Table 7). The radioactive material extractable from the fish remained at the origin of the TLC plate, indicating the polar nature of the radioactivity. The continued use of phenmedipham should not lead to its accumulation in aquatic food chains.

2,4-D, or 2,4-dichlorophenoxyacetic acid, is one of the oldest synthetic herbicides in use today. After more than 30 years of its continued use, problems relating to aquatic food-chain accumulation of 2,4-D are nonexistent. The data from the experiment with ¹⁴C-2,4-D corroborate the "outdoor" data that have accumulated for the past three decades, as no 2,4-D residues were found in any of the organisms of the model ecosystem (Table 8). As might be expected, the alga contained the greatest number of unidentifiable ¹⁴C residues even though eight standard degradation products of 2,4-D were cochromatographed. Continued use of 2,4-D does not appear to lead to environmental problems relating to its accumulation in aquatic food chains. "Real-world" data and model ecosystem results are similar and clearly demonstrate the ability of this microcosm to predict potential environmental problems.

Propachlor, or 2-chloro-*N*-isopropylacetanilide, is one of a large number of *α*-chloroacetanilide herbicides, which

include alachlor, that are used to control annual grasses and some broadleaf weeds in a number of crops including corn and soybeans. The structural similarity of propachlor to alachlor and its great susceptibility to degradation are evident, as none of the organisms contained residues of this herbicide (Table 9). There was a very minute amount of propachlor (0.0564 ppb) in the water at the end of the experiment. Clearly the α -haloacetanilides are some of the most degradable herbicides examined in this system, and continued use of these herbicides should not lead to their accumulation in aquatic food chains.

Pyrazon, or 5-amino-4-chloro-2-phenyl-3-(2H)-pyridazinone, is used for the control of annual broadleaf weeds in sugar beets and beets. The model ecosystem data clearly demonstrate that pyrazon is susceptible to degradation, as only the crab contained residues (0.476 ppm) of this herbicide, which constituted 95.4 percent of the radioactive materials extractable from the crab (Table 10). The EM value for the pyrazon in the crab was 22.5 (Yu et al. 1975b). Continued use of this herbicide would not appear to lead to problems related to accumulations of it in aquatic food chains.

Trifluralin, or α,α,α -trifluoro-2,6-dinitro-*N,N*-dipropyl-*p*-toluidine, is used to control grasses and several broadleaf weeds in soybeans, cotton, and many other crops. Only the snail and fish contained 5.046 ppm and 0.261 ppm, respectively, of trifluralin as an extractable residue (Table 11). The percentages of trifluralin in the extractable radioactive materials in the snail and fish were 75.7 and 34.0, respectively. The EM values for the snail and fish were 17,872 and 926, respectively. In addition to trifluralin the snail contained lesser amounts of α,α,α -trifluoro-2,6-dinitro-*N*-propyl-*p*-toluidine (0.337 ppm), which had an EM value of 3,874. Trifluralin is the only

herbicide tested that showed a propensity to accumulate in either the fish or snail. Its tendency to accumulate is undoubtedly related to its low water solubility (0.58 ppm) and high lipid solubility (Probst & Tepe 1969). Despite the accumulation in the snail and fish, trifluralin is unusual in that it is susceptible to degradation, forming at least 11 degradation products in water, yet demonstrates a tendency to be magnified to some extent through aquatic food chains. It is not, however, magnified at the level of chlorinated hydrocarbons, but at a level very similar to that of the insecticide methoxychlor, which has an EM value of about 1,500.

Metribuzin, or 4-amino-6-*tert*-butyl-3-(methylthio) *as*-triazin-5-(4*H*)-one, is a new herbicide used for weed control in soybeans. The data in Table 12 clearly demonstrate the degradability of this herbicide in the model ecosystem, as no residues of this herbicide were isolated from the organisms. Further, the water contained numerous metabolites, which is indicative of the susceptibility of this herbicide to degradation under the conditions of this experiment. The major degradation product in the water is a mixture of DK and DADK, which were not resolvable by thin-layer chromatography. The data from this system clearly indicate that the continued use of this herbicide should not lead to its accumulation in aquatic food chains.

Bifenox, or methyl-5-(2',4'-dichlorophenoxy)-2-nitrobenzoate, is a new pre-emergence herbicide somewhat related to 2,4-D. As shown in Table 13, bifenox is degraded by hydrolysis of the methyl ester to form the parent benzoic acid (compound B, Table 13), and by reduction of the nitro group to the corresponding amino compound (compound A, Table 13). There was no evidence of cleavage of the diphenyl ether moiety. Bifenox is of low water solubility (0.35 ppm) (Fig. 2) and was bioconcentrated about 200-fold by the

fish. It falls in the borderline area of moderate biodegradability and should be used with care.

ORGANOPHOSPHORUS INSECTICIDE TEST RESULTS

The decline in the use of organochlorine insecticides to control pest species (Table 1) is the result of factors such as target-pest resistance, environmental hazards, and more recently, the ban imposed by the U.S. Environmental Protection Agency (EPA) on DDT and aldrin/dieldrin as general insecticides for home and agricultural use. Further, in view of the recent action of the EPA seeking to ban the use of chlordane, heptachlor, and heptachlor epoxide, it is certain that more phosphate and carbamate insecticides will be used to fill the void left by the elimination of the organochlorine insecticides. Therefore, it is essential to examine carbamate and phosphate insecticides to insure that no problems of the environmental persistence and aquatic food-chain accumulations of these insecticides will occur.

Chlorpyrifos, or *O,O*-diethyl-*O*-(3,5,6-trichloro-2-pyridyl) phosphorothionate, had EM values in the alga, snail, mosquito, and fish of 72, 691, 45, and 320, respectively. Of the radioactive material extractable from each organism, the percentages of chlorpyrifos isolated from the alga, snail, mosquito, and fish were 30.3, 48.1, 7.9, and 49.5, respectively (Table 14). The position of the ^{14}C label in the pyridyl ring allows the investigation of the persistence of this moiety in the organisms of the system or its uptake by them or both. The ecological magnification and percentage of the extractable radioactive materials for the pyridinol in each organism were: alga, 44, 18.8 percent; snail, 443, 32.3 percent; mosquito, 191, 34.9 percent; and fish, 180, 29.1 percent. The absence of the oxon of chlorpyrifos in any of the organisms is typical, as the oxons of the phosphate

insecticides were not found generally in any of the organisms.

Chlorpyrifos-methyl is an insecticide similar to chlorpyrifos except for the substitution of *O,O*-dimethyl for *O,O*-diethyl groups to yield *O,O*-dimethyl-*O*-(3,5,6-trichloropyridinyl) phosphorothionate. The chlorpyrifos-methyl ecological magnification values for the alga, snail, mosquito, and fish are 478, 544, 1,875, and 95, respectively. The values for the snail and fish are substantially lower than those found in the organisms subjected to chlorpyrifos, the result of the greater susceptibility of the *O*-methyl groups to degradation as compared to that of the *O*-ethyl moieties in chlorpyrifos. The percentages of chlorpyrifos-methyl in the radioactive materials isolated from the alga, snail, mosquito, and fish were 49.0, 49.3, 68.2, 20.7 percent, respectively (Table 15). Again, because the ^{14}C label is located in the pyridyl moiety, it is possible to investigate the fate of this group in the model ecosystem. The ecological magnification and percentage of the chlorinated pyridinol in the organisms were: snail, 41, 9.3 percent; fish, 54.5, 29.7 percent. As was observed for chlorpyrifos, none of the organisms contained the activation product, chlorpyrifosoxon-methyl.

Counter® is one of the newer phosphate insecticides under development for use as a soil insecticide, and it has the chemical name of *O,O*-diethyl *S*-(*tert*-butylthio)-methyl phosphorodithioate. This insecticide was therefore applied in the sand of the model ecosystem to mirror its use in the field. The similarity in structure to phorate (Thimet®) and disulfoton (Di-Syston®) is obvious, and the degradation in pathways of sulfur oxidation in the side chain of Counter® was similar to those of the other two pesticides. The percentages of Counter® in the radioactive materials extractable from the alga, snail, mosquito, and fish were 3.3, 23.5, 4.7, and 25.0, respectively (Table

16). No other metabolites were isolated from the fish or mosquito although a small amount (0.0241 ppm) of Counter® oxon was observed in the snail. The Counter® ecological magnification values from the alga, snail, mosquito, and fish were 175, 1,830, 360, and 535, respectively. These values from the fish and snail are somewhat higher than those found for most other phosphate insecticides. Undoubtedly these higher values are related both to the initial stability of the phosphorodithionate and to the application of this chemical to the sand, which does not allow for the initial metabolism and degradation by the caterpillars. The water sector of the ecosystem contained only trace amounts of Counter® and of nearly all of the possible combinations of the oxidation products of phosphorothioate and sulfide sulfur.

Temephos (Abate®), or the bis-*O,O*-dimethylphosphorothioate ester of 4,4'-dihydroxydiphenyl sulfide, is an excellent mosquito larvicide and appears to possess ideal environmental characteristics, as it is exceptionally degradable. No residues of temephos or any of its oxidative or hydrolytic metabolites occurred in the fish. Because of its high larvicidal activity, the mosquitoes were killed throughout the usual duration of the experiment, and it was extended to 53 days. The alga and snail contained small amounts (0.00195 and 0.01876 ppm, respectively) of temephos (Table 17). The EM values of temephos from the alga and snail were 1,500 and 14,431, respectively. In addition, the alga contained small amounts (0.4-2.0 ppb) of all of the cochromatographed metabolites, and the snail contained substantially fewer of the metabolites though at somewhat higher concentrations (2-27 ppb). The higher concentrations in the snail again emphasize the low titer of enzymes in this organism capable of degrading foreign compounds. The absence of data for the mosquito

emphasizes the outstanding larvicidal properties of this insecticide.

Fonofos (Dyfonate®), or *O*-ethyl-S-phenyl ethylphosphonodithioate, is an effective soil insecticide which is finding increasing use as a replacement for the organochlorine insecticides. Although the organisms of the model ecosystem contained small amounts of the unchanged fonofos, none contained significant amounts of degradation products (Table 18). The percentages of fonofos in the radioactive materials extractable from the alga, snail, and fish were 32.1, 27.0, and 80.5, respectively. Further, the fonofos in the alga, snail, and fish had EM values of 108, 86, and 77, respectively. The large number of degradation products isolated from the water (14), coupled with the very low EM values, clearly indicates that fonofos does not accumulate significantly in aquatic food chains.

Fenitrothion, or *O,O*-dimethyl-*O*-(3-methyl-4-nitrophenyl) phosphorothioate, is one of the safest organophosphorus insecticides, as the LD₅₀ for the rat is 500 mg per kg and for the mouse is 1,200 mg per kg. The substitution of the methyl group in the *meta* position of the nitrophenyl ring of methyl parathion is believed to be responsible for the much reduced mammalian toxicity as compared to that of methyl parathion, of which the LD₅₀ for the rat is 13 mg per kg and for the mouse is 75 mg per kg. Fenitrothion EM values of 349, 2.2, and 9.8 were found for the alga, mosquito, and fish, respectively. The percentages of fenitrothion in the radioactive materials isolated from the alga, mosquito, and fish were 33.7, 6.6 and 44.4, respectively (Table 19). The only other degradation product isolated from the organisms was a small amount (5.7 ppb) of fenitroxon found in the fish. This degradation product of fenitrothion had an EM value of 6.5. The isolation of this phosphorus oxon from the fish is

unique, as none of the other oxons of the phosphate insecticides were found in the fish.

Malathion, or *O,O*-dimethyl-*S*-(1,2-dicarboethoxyethyl)-phosphorodithioate, is widely used in the home and garden as an insecticide. It appears to be exceptionally degradable, as no traces were found in any of the model-ecosystem organisms (Table 20). The fish, snail, and mosquito contained several uncharacterized metabolites, which were also found in the water. It is apparent that malathion is one of the most degradable organophosphorus insecticides examined in this system. This degradability, together with malathion's low mammalian toxicity (rat oral LD_{50} , 1,300 mg per kg), makes it a safe and useful product.

Acephate (Orthene®), or *O*-methyl-*S*-methyl-*N*-acetylphosphoramidothioate, is a relatively new insecticide, which has found widespread use in the control of pests of vegetables. The parent insecticide was not isolated from any of the model-ecosystem organisms (Table 21), which is not unexpected in view of the high water solubility of acephate (650,000 ppm). However, an uncharacterized degradation product was isolated (R_f 0.93) in all of the organisms except the clam and fish. In the crab this degradation product had an EM value of 4,273 times the concentration in the water. Further research is in progress to determine the structure of this degradation product.

Leptophos (Phosvel®), or *O*-(4-bromo-2,5-dichlorophenyl)-*O*-methyl phenylphosphonothionate, is a new organophosphate insecticide now undergoing extensive development for use in controlling pests of cotton and vegetable crops. The available environmental degradation information (Holmstead et al. 1973; Aharonson & Ben-Aziz 1974) clearly indicates that this insecticide has a high degree of environmental stability. Other problems with this insecticide have been found in its use in

Egypt on cotton, where it killed 1,300 water buffaloes (Shea 1974). Laboratory experiments with chickens have shown that leptophos has neurotoxic effects (Abou-Donia et al. 1974).

The behavior of leptophos in our model ecosystem indicates that it is one of the most persistent phosphorus-derived pesticides examined (Table 22). The experiment was extended to 45 days, because each time the mosquitoes were introduced, they immediately died. Even though the mosquitoes died after their introduction on the 45th day, the fish were then added to the ecosystem, and the experiment was terminated 3 days later. Every organism contained residues of leptophos, the alga having 13,221 ppm, the snail 52.27 ppm, and the fish 1,559 ppm. These residues of leptophos in the radioactive materials extracted from the alga, snail, and fish constituted 41.8, 97.3, and 83.5 percent, respectively, of the totals. The EM values for leptophos were 12,243 for the alga, 48,398 for the snail, and 1,444 for the fish, respectively. Clearly, this is the most persistent organophosphorus insecticide examined in the model ecosystem.

Parathion, or *O,O*-diethyl *O*-4-nitrophenyl phosphorothionate; and methyl parathion, its *O,O*-dimethyl analogue, were produced in the United States in 1970 in the combined amount of about 56 million pounds. The available information on the behavior of parathion and methyl parathion in the environment indicates that they have presented no problems of accumulation in aquatic food chains after more than 25 years of widespread use. The model-ecosystem data (Table 23) corroborate the outdoor data. The only organism containing a residue of parathion was the fish, and there the concentration was only 0.1006 ppm, which constituted about 52 percent of the radioactive materials isolated from the fish. The experiment was lengthened to 38 days because of the toxicity of the water to

the mosquito. The use of $2,6\text{-}^{14}\text{C}$ -labeled 4-nitrophenol-labeled parathion allowed the examination of the fate of this moiety, and it was determined that the water (0.000136 ppm) and fish (0.0086 ppm) contained small amounts of this moiety.

CARBAMATE INSECTICIDE TEST RESULTS

The carbamate insecticides recently have assumed a large role in Illinois agriculture with the elimination of the organochlorine insecticides because of the resistance of target pests, the environmental accumulative tendency of the organochlorine compounds, and their carcinogenic properties. The use of metalkamate, carbofuran, and carbaryl to control insect pests on corn and soybeans has proved to be effective and has eliminated the aquatic food chain accumulation problems of the formerly used chlorinated hydrocarbon insecticides.

Metalkamate is a 3:1 mixture of *m*-(1-ethylpropyl)-phenyl and *m*-(1-methylbutyl)-phenyl *N*-methylcarbamates introduced to control soil pests of corn. This insecticide does not have any tendency to accumulate in the higher members of the trophic web, though the alga (0.980 ppm); crab (0.0498 ppm), which died 7 days after the introduction of metalkamate; and *Elodea* (0.245 ppm) contained residues of the parent compound (Table 24). These residues of metalkamate in the alga, crab, and *Elodea* constituted 55.0, 17.4, and 25.9 percent, respectively, of the extractable radioactive material from these organisms. The most interesting observation here is that these three organisms were the only organisms that contained detectable amounts of ^{14}C . None of the other organisms had substantial amounts of ^{14}C residues. While this insecticide has not been as effective recently as it has been in the past in controlling pests of corn, its environmental behavior in the model

ecosystem clearly indicates that should it become widely employed, no aquatic food chain accumulation problems are likely to arise.

Carbaryl, or 1-naphthyl *N*-methylcarbamate, was the first carbamate insecticide to find widespread use in the home garden and in agriculture, and it is presently the most widely used insecticide in the United States. With the banning for general use of DDT in 1972, carbaryl is being used to control the tussock moth in the Pacific Northwest; the gypsy moth, which is migrating westward from the eastern regions of the United States; and the spruce budworm. After more than 20 years of widespread use, neither problems of accumulations in food chains nor of ubiquitous food residues have been experienced. The data from the terrestrial-aquatic model ecosystem (Table 25) definitely corroborate the experience in the field, as no residues of carbaryl were found in any of the organisms. The water contained many degradation products of carbaryl, but no residues of carbaryl itself. Continued widespread use of this insecticide will definitely not lead to problems associated with accumulations in aquatic food chains.

Carbofuran, or 2,2-dimethyl-2,3-dihydrobenzofuranyl-7-*N*-methylcarbamate, is an excellent soil insecticide for the control of corn and soybean pests. The behavior of this carbamate insecticide is similar to that of the other carbamates examined in that none of the organisms in the model ecosystem contained residues of the parent insecticide (Table 26). The water contained a small amount of carbofuran (0.003889 ppm) as well as trace amounts of other metabolites and degradation products of carbofuran (Yu et al. 1974). It appears that the continued use of this insecticide will not lead to environmental problems of accumulations in aquatic food chains.

Propoxur, or 2-isopropoxyphenyl *N*-methylcarbamate, is used for household

pest control and for residual spraying for adult mosquitoes. In the model system every organism contained residues of propoxur at concentrations of 0.0360, 0.0928, 0.4441, and 0.0468 ppm for the alga, snail, mosquito, and fish, respectively (Table 27). The percentages of propoxur in the radioactive materials extracted from the alga, snail, mosquito, and fish were 7.8, 23.5, 19.4, and 39.9, respectively. The EM values for the alga, snail, mosquito, and fish are 112, 290, 1,388, and 146, respectively. In addition to the parent compound, the fish contained lesser amounts of 2-isopropoxyphenol (0.0252 ppm) and 2-isopropoxyphenyl *N*-hydroxymethyl carbamate (0.0180 ppm). Propoxur was the only carbamate examined in this model ecosystem that was accumulated by the fish. This fact may be, in part, related to the high specific activity of the radiolabeled propoxur (10.4 mCi/mM), which made it possible to determine the small residues of this insecticide in the organisms.

Aldicarb is a systemic carbamate insecticide, 2-methyl-2-methylthiopropionaldoxymyl *N*-methylcarbamate. Aldicarb is readily oxidized *in vivo* to sulfide and sulfone metabolites, both of which are insecticidal. These metabolites and the parent compound form relatively persistent systemic toxicants in plant tissues (Metcalfe et al. 1966). A single application to the roots of cotton plants kills boll weevil larvae during an entire growing season. Therefore, it was not unexpected to find these products persisting over the 33-day period of the model-ecosystem experiment (Table 28). However, the substantial water solubility of aldicarb, 0.6 percent, clearly prevented high bio-magnification in the organisms, and the EM value in the fish was 42. Aldicarb was highly toxic to the snail, *Physa*, and all of these died early in the course of the experiment.

Formetanate, or 3-dimethylamino-methyleneiminophenyl *N*-methylcarba-

mate•hydrochloride, is a carbamate acaricide. As shown in Table 29, this compound is highly biodegradable, and no trace of the parent compound was found in the model ecosystem after 33 days. The only identifiable degradation product (compound A, Table 29) involved removal of the *N*-methylcarbamoyl group and loss of the amidino moiety. We do not expect that this compound will cause problems in environmental quality.

MISCELLANEOUS INSECTICIDE TEST RESULTS

Methoprene, or isopropyl-11-methoxy-3,7,11-trimethyldodeca-2,4-dienoate, is one of the "fourth-generation" insecticides believed to interfere with the normal metamorphic development of insects. This pesticide has shown some promise in the control of mosquitoes developing in irrigated fields in California. The degradation of methoprene has been examined in detail in several outdoor systems (Quistad et al. 1974 and 1975; Schooley et al. 1975). In the model ecosystem every organism contained residues of methoprene (Table 30), with the alga containing 2.220 ppm, the snail 1.500 ppm, and the fish 0.0176 ppm. These methoprene residues in the alga, snail, and fish constituted 48.0, 30.7, and 25.1 percent, respectively, of the radioactive materials extracted from each organism. The EM values for methoprene in the alga, snail, and fish were 25,814, 17,442, and 205, respectively. Measurable amounts of the 11-*O*-demethylated methoprene were isolated from the alga, 0.723 ppm; snail, 0.469 ppm; and fish, 0.0181 ppm though the water contained none of this degradation product. Finally, the water, snail, and fish contained small amounts of 11-hydroxy-3,7,11-trimethyldodeca-2,4-dienoic acid.

Dimilin, or 1-(2,6-difluorobenzoyl)-3-(4-chlorophenyl) urea, is a recently introduced insecticide which apparently interferes with the normal development

of the insect cuticle and leads to mortality at molting. The use of two different ^{14}C -labeled sites in dimilin enabled us to examine the fates of the two phenyl moieties. Every organism contained this insecticide (Table 31), from the high of 13.1369 ppm in the mosquito in the ^{14}C -chlorophenyl urea dimilin to the low of 0.1097 ppm in the fish in the ^{14}C -difluorobenzoyl dimilin. Despite the variation in the absolute quantity of dimilin in the fish of the two experiments, 0.1097 ppm for the ^{14}C -difluorobenzoyl and 0.3193 ppm for the ^{14}C -chlorophenyl urea, the EM values of 19.2 and 14.5 were very close. The percentage of dimilin in the extractable radioactive materials isolated from the fish was 6.7 percent for ^{14}C -difluorobenzoyl dimilin and 5.3 percent for ^{14}C -chlorophenyl dimilin, indicating again close agreement in the data for the two ^{14}C labels. While dimilin amounted to a small percentage of the extractable radioactive materials in the fish, the fractions of dimilin were considerably higher (46–98 percent) in the radioactive materials isolated from the rest of the organisms.

Chlordimeform, or *N*-(4-chloro-*o*-tolyl)-*N,N*-dimethylforamidine, is one of the newer insecticides and appears to be effective in controlling cotton pests. In the model ecosystem only the snail contained residues of this insecticide, with a concentration of 0.0710 ppm (Table 32). The fraction of chlordimeform in the extractable radioactive materials isolated from the snail was about 40 percent. The water contained numerous breakdown products of chlordimeform, clearly indicating the lability of this insecticide in the model ecosystem.

Banamite®, or benzoylchloride-2,4,6-trichlorophenylhydrazone, is a new pesticide that has found use on citrus for the control of mites (Table 49). Only the crab (0.0156 ppm), aquatic plant (0.041 ppm), and mosquito (0.0736 ppm) contained residues of this pesticide. The EM values for banamite in these organisms were 839 for

the crab, 2,204 for the aquatic plant, and 3,957 for the mosquito. The amount of banamite in the extractable radioactive materials from these organisms ranged from 1 to 2 percent. Though neither the fish nor the snail contained residues of banamite, they contained an unidentified degradation product, designated II, that was magnified about 20,000 times in the snail and about 3,000 times in the fish. It does not appear that continued use of this pesticide will lead to problems of aquatic food-chain accumulation, but perhaps more detailed analysis of the chemical structure of some of the degradative products should be undertaken.

ORGANOCHLORINE INSECTICIDE TEST RESULTS

The organochlorines, especially the cyclodienes aldrin, heptachlor, and chlordane, have been used extensively in Illinois since they were introduced in 1954 for the control of underground insect pests of corn, particularly the corn rootworms *Diabrotica longicornis* and *D. undecimpunctata howardi* (Bigger & Blanchard 1959). Their use as soil treatments increased from about 125,000 acres (5.06×10^4 ha) treated in 1954 to a maximum of 5,601,572 acres (2.27×10^6 ha) treated in 1966 and slowly declined to about 2,100,000 acres (8.51×10^5 ha) treated in 1974 (Petty 1974). The average treatment rate is about 1.6 pounds per acre (1.76 kg per ha) of technical material for aldrin and 2.0 pounds (2.2 kg per ha) for heptachlor (U.S. EPA 1972a). It is estimated that over the 20-year period more than 82 million pounds (3.73×10^7 kg) of these chemicals have been applied to Illinois farm soils (Illinois Natural History Survey data). The approximate farm acreages treated with the organochlorine insecticides in Illinois are presented in Table 1 (Illinois Cooperative Crop Reporting Service 1973).

The use of cyclodiene insecticides in Illinois has been complicated by the

invasion of the western corn rootworm, *D. virgifera*, which now covers nearly all of the cornland of Illinois and is totally resistant to the toxic action of aldrin, heptachlor, and chlordane (Petty & Kuhlman 1972), and by the unpredictability of attacks by the black cutworm, *Agrotis ipsilon*.

ENVIRONMENTAL PERSISTENCE

The organochlorine insecticides in use in Illinois are generally environmentally persistent or are readily converted to environmentally persistent compounds by photochemical or microbial action or *in vivo* in the tissues of plants and animals. This is particularly true of the oxidation of aldrin to its 6,7-epoxide, dieldrin; heptachlor to its 2,3-epoxide, heptachlor epoxide; and the *cis*- and *trans*-chlordane isomers to oxychlordane. The average times required for 95-percent "breakdown" of these compounds in the soil has been estimated as: DDT, 11 years; dieldrin, 9.7 years; lindane, 6.7 years; chlordane, 4.2 years; heptachlor, 3.5 years; and aldrin, 2.5 years (Edwards 1965). Therefore, because of extremely heavy use patterns, it is no surprise to find that Illinois soils have been relatively highly contaminated by these compounds. The National Soils Monitoring Program (Carey et al. 1973) has reported these concentrations in Illinois soils: aldrin, 0.01–0.83 (average 0.07) ppm; chlordane, 0.05–1.32 (average 0.09) ppm; dieldrin, 0.01–1.08 (average 0.14) ppm; and DDT(T), 0.06–0.12 (average >0.01) ppm. These residues were among the highest found in the United States.

DDT, or 2,2-bis-(*p*-chlorophenyl)-1,1,1-trichloroethane, has the highest potential for bioaccumulation, 84,500-fold from water to fish, of any of the compounds studied (Metcalf et al. 1971). This tendency to accumulate is the result of DDT's low water solubility (0.0012 ppm) and its environmental stability. DDT also accumulates because of its partial conversion by dehydrochlorination to DDE, 2,2-bis-(*p*-chlorophenyl)-1,1-dichloroethylene

(water solubility 0.0013 ppm). In the fish at the top of the food chain DDT constituted 34.3 percent, DDE 53.9 percent, and DDD 9.8 percent of the absorbed total ¹⁴C-radiolabeled material (Table 33). This fact demonstrates the gravest environmental flaw in the use of DDT, i.e., the conversion to and storage in animal lipids of the highly persistent DDE. DDE constituted 52.0 percent of the total radioactive materials in the snail, 58.4 percent in the mosquito, and 54.0 percent in the fish. The percentage of unextractable radioactive materials in the various organisms, a measure of total environmental stability, was low, ranging from 0.25 percent in the mosquito to 13.5 percent in the alga, and averaging 3.9 percent for all test organisms. As shown in Table 34, DDE in the model ecosystem was degraded slowly and showed high ecological magnification.

Because of its persistence, degradation to the even more stable DDE, bioaccumulation, and effectiveness in inducing microsomal oxidase enzymes (Peakall 1970), DDT has been banned as an insecticide by both the U.S. and Illinois Environmental Protection Agencies. The high degree of bioconcentration and the preponderance of storage as DDE found in the model ecosystem study are representative of the values found in nature, e.g., fatty tissues of humans in the USA contain an average of about 2.3–4.0 ppm of DDT and 4.3–8.0 ppm of DDE (Durham 1969). DDT in Lake Michigan at a concentration of 0.000006 ppm is biomagnified in lake trout to levels of 10–28 ppm (U.S. EPA 1972*b*), and in herring gulls to 99 ppm (Hickey et al. 1966). The lake trout residues averaged 53 percent DDE, 15 percent DDD, and 32 percent DDT (U.S. EPA 1972*b*). DDT applied to a marsh in New Jersey for mosquito control was found in fish at 0.17–2.07 ppm and in gulls at 75 ppm (Woodwell et al. 1967).

DDD, or 2,2-bis-(*p*-chlorophenyl)-1,1-dichloroethane, exhibited similar model-ecosystem behavior to that of

DDT (Table 35) and is, in fact, a degradative product of DDT (Table 33). DDD constituted 58.9 percent of the total extractable radioactive materials in the snail, 59.0 percent in the mosquito, and 85.4 percent in the fish (Metcalf et al. 1971). Thus, although DDD is a step on the degradative pathway of DDT and does not form the environmentally recalcitrant DDE, DDD seems to offer only slight improvement over DDT in regard to environmental hazard. Its ultimate fate in higher animals is conversion to and excretion as DDA (4,4'-dichlordiphenyl acetic acid), but this is an extremely slow process. DDD applied to Clear Lake, California, to control the Clear Lake gnat, *Chaoborus astictopus*, was found to be bioconcentrated through food chains from 0.02 ppm in the water to 903 ppm in the fat of plankton-eating fish and to 2,690 ppm in the fat of carnivorous fish (Hunt & Bischoff 1960).

Methoxychlor, or 2,2-bis-(*p*-methoxyphenyl)-1,1,1-trichloroethane, differs from DDT in two important ways. It is 500 times more soluble in water, and the aryl CH_2O groups (degradophores) are readily biodegradable to OH groups, further increasing the polarity and water solubility. Thus, as shown in Table 36, methoxychlor is much less accumulative than DDT is in most animals. Methoxychlor amounted to 84.0 percent of the total extractable radioactive materials in the snail and 51.5 percent in the fish. In contrast to the ready conversion of DDT to DDE (Table 33) and the storage of the latter in animal tissues, only very small amounts of the corresponding methoxychlor ethylene are stored by animals. The principal degradation pathway for methoxychlor is through conversion to the mono-OH and di-OH derivatives, which are readily converted to polar conjugation products in animals (Metcalf et al. 1971).

Methoxychlor is classed as a moderately persistent insecticide and does

not accumulate to high levels in most animal tissues or milk.

It offers a severe toxic hazard to fish but is degraded in fish much more readily than is DDT (Reinbold et al. 1971). When used for control of the elm bark beetle, *Scolytus multistriatus*, vector of Dutch elm disease, methoxychlor has not resulted in environmental problems of transfer from earthworms to birds, as has DDT (Hunt & Sacho 1969).

Aldrin, or 1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1,4-*endo*, *exo*-5,8-dimethanonaphthalene, is rapidly converted in the model ecosystem and its organisms to the very persistent 6,7-epoxide, dieldrin (Table 37). In the model ecosystem treated with aldrin, dieldrin was stored as 85.7 percent of the total extractable radioactive materials in the alga, 91.6 percent in the snail, and 95.8 percent in the fish (Metcalf et al. 1973). The bioaccumulation of both aldrin and dieldrin is high, directly proportional to their water insolubility, but not as high as that of DDT and DDE. Only minor amounts of two degradation products, 9-keto dieldrin and 9-hydroxy dieldrin, were found, attesting to the stability of dieldrin, and these two products were also concentrated in the alga, snail, and fish. The ultimate degradative pathway is through *trans*-dihydroxydihydro aldrin. Aldrin, because of its rapid conversion to the highly persistent dieldrin, its bioaccumulation, and its carcinogenicity (Walker et al. 1973), has been banned as an insecticide by the U.S. Environmental Protection Agency.

Dieldrin. When the model-ecosystem evaluation of dieldrin, the 6,7-epoxide of aldrin, was begun (Table 38), little difference was found between it and the evaluation of aldrin (Table 37). Dieldrin is slightly more water soluble than aldrin and exhibited slightly lower bioconcentrations in the fish. The stability of dieldrin was shown by the storage of dieldrin as 98.7 percent of the extractable radioactive materials in

the alga, 99.0 percent in the snail, and 97.8 percent in the fish (Sanborn & Yu 1973). However, 9-OH and 9-C=O dieldrin were identified as important degradation products along with *trans*-dihydroxydihydro aldrin.

The several thousandfold accumulation of dieldrin in the fish of the model ecosystem following the application of aldrin is in agreement with observations in nature. Humans in the USA have average values of 0.29–0.31 ppm of dieldrin in fatty tissues (Durham 1969). Dieldrin in Lake Michigan at a concentration of 0.000002 ppm in water is biomagnified in lake trout to levels of 0.14–0.45 ppm (U.S. EPA 1972*b*). The average bioconcentration of dieldrin from the waters of Illinois farm ponds to the tissues of fish was 5,000- to 20,000-fold (W. F. Childers & W. N. Bruce, Illinois Natural History Survey, unpublished data).

Toxaphene has been shown to be a mixture of at least 177 components (Holmstead et al. 1974) about two-thirds of which are $C_{10}H_{11}Cl_7$, $C_{10}H_{10}Cl_8$, and $C_{10}H_9Cl_9$ compounds. The highly insecticidal components are heptachlorobornanes (Casida et al. 1974). The ^{14}C -radiolabeled toxaphene used in the model-ecosystem experiments was supplied by the manufacturer as the chlorination product of $\{8\text{-}^{14}C\}$ camphene to 67–69 percent Cl (sample X19093-4-2K) and is presumably representative of the technical product. As shown in Table 39, the ^{14}C -radiolabeled toxaphene behaved in a surprisingly homogenous fashion in the extracts from the organisms of the model ecosystem. The major ingredients referred to as "toxaphene" (R_f 0.70) were highly persistent and accumulated to several thousandfold levels in the organisms of the system. "Toxaphene" constituted 82.6 percent of the total extractable radioactive materials in the alga, 86.6 percent in the snail, 62.7 percent in the mosquito, and 64.9 percent in the fish. The unextractable ^{14}C -labeled materials averaged 19 percent of the total radio-

active materials in all of the organisms. Thus, toxaphene exhibited model-ecosystem behavior rather like that of endrin (Table 40).

The behavior of toxaphene in the environment is little known because its enormous number of constituents poses almost insurmountable analytical problems. Toxaphene in Big Bear Lake, California, at 0.2 ppm was found to be biomagnified to 200 ppm in goldfish (Hunt & Keith 1963), and in Lake Poinsett, South Dakota, from 0.001 ppm in the water to 0.176 ppm in the tissue and 1.152 ppm in the fat of the carp, *Cyprinus carpio* (Hannon et al. 1970). These instances of thousandfold biomagnification are in perfect agreement with the model ecosystem results.

Endrin is a highly water-insoluble pesticide that was also bioconcentrated in the organisms of the model ecosystem to a high degree (Table 40). Endrin, or 1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-*endo,endo*-5,8-dimethanonaphthalene, is the *endo,endo*-isomer of dieldrin and is less environmentally persistent than dieldrin. Endrin was stored as 84.9 percent of the total extractable ^{14}C -labeled materials in the alga, 83.0 percent in the snail, and 75.9 percent in the fish. Degradation appeared to be largely through an unknown compound designated II, probably 9-OH endrin in analogy with dieldrin. Unknown compound III is probably 9-C=O endrin (Metcalf et al. 1973).

Biological observations on the organisms of the system were particularly informative. Endrin was not only highly toxic to the salt-marsh caterpillar, which had difficulty consuming the treated sorghum leaves, but repeatedly killed all the daphnia, mosquito larvae, and fish in the aquatic portion of the system. The high toxicity of the water phase persisted for more than 60 days from the beginning of the experiment and occurred at endrin concentrations of 0.001–0.002 ppm. Because of this toxicity the experiment was extended

to nearly twice the usual 33-day period, and thus the data in Table 40 were measured after 63 days. Fish added to the model system had violent convulsions within 10–15 minutes after being placed in the contaminated water. These biological observations demonstrated the substantial predictive value of the model-ecosystem investigations and could have given a preview of the Mississippi River fish kills associated with the leaching of endrin wastes (Barthel et al. 1969). Endrin, because of its great bioaccumulation, persistence, and extremely high toxicity to a wide variety of organisms, is a highly dangerous insecticide.

Lindane, or gamma-1,2,3,4,5,6-hexachlorocyclohexane, has a higher water solubility than many of the other organochlorine insecticides and appears to be less readily bioconcentrated in animal tissues (Table 41). In the model ecosystem lindane was stored as 20.6 percent of the total extractable radioactive materials in the snail and 91.7 percent in the fish. None could be detected in the alga or the mosquito. The principal degradation product appeared to be gamma-pentachlorocyclohexene. Lindane is substantially more biodegradable than DDT and the cyclo-diene pesticides, and it appears to be degraded environmentally to a series of trichlorophenols (Metcalf et al. 1973).

BHC residues have been found widely distributed in human fatty tissues in the USA at 0.20–0.60 ppm (Durham 1969). The *beta*-isomer (an ingredient of technical BHC insecticide) is the most persistent isomer of lindane, and the environmental persistence of the *gamma*-isomer (lindane) is not well understood.

Mirex, dodecachloro-octahydro-1,3,4-metheno-2H-cyclabuta-{c,d}-pentalene, was one of the least degradable compounds that we evaluated and was stored as 97.8 percent of the total extractable radioactive materials in the alga, 99.4 percent in the snail, 99.6 percent in the mosquito, and 98.6 percent

in the fish (Table 42) (Metcalf et al. 1973). It is clearly a highly persistent pollutant and showed a substantial degree of bioaccumulation. Mirex is of environmental importance, as it is one of the most effective inducers of microsomal oxidase enzymes. Mirex, following its widespread use as a bait for the fire ant, has been found in tissues of wild birds at levels of up to 3 ppm and in rodents at nearly 20 ppm (Unpublished data). It has also been found in tissues of northern pike and long-nose gar from Lake Ontario at 0.020–0.050 ppm (Kaiser 1974).

Heptachlor, or 1-*exo*-4,5,6,7,8-heptachloro-3a,4,7,7a-tetrahydro-4,7-methanoindene, has a low level of water solubility and a high potentiality for bioaccumulation (Table 43). Heptachlor is rapidly converted in the model ecosystem and its organisms to the very persistent 2,3-epoxide, heptachlor epoxide. In the model ecosystem heptachlor epoxide was stored as 59.1 percent of the total extractable radioactive materials in the alga, 45.6 percent in the snail, and 60.6 percent in the fish. These values are considerably lower than the corresponding values for the storage of dieldrin after the treatment of crops with aldrin (Table 37) and reflect the existence of an alternate degradative pathway in heptachlor, the replacement of the 1-Cl atom by OH to give 1-hydroxy-chlordene. This degradative product is more polar and water soluble than heptachlor and is not as highly accumulative. It can also be epoxidized *in vivo* to the 2,3-epoxide, 1-hydroxy-chlordene epoxide, which was found stored in the snail, mosquito, and fish. This latter degradative product could also be formed by hydrolysis of heptachlor epoxide. Heptachlor epoxide in the model ecosystem (Table 44) showed a persistence comparable to that of dieldrin (Table 38).

In the heptachlor test the unextractable ¹⁴C-labeled materials averaged 29 percent of the total radioactive materials in the various organisms. Hepta-

chlor epoxide is widely distributed in the environment, and the average level in the body fat of humans in the USA is 0.1–0.24 ppm (Durham 1969). Yellow perch from Lake Michigan had heptachlor epoxide body residues ranging from 0.060 to 0.097 ppm (U.S. EPA 1972b). Heptachlor and heptachlor epoxide are under surveillance by the U.S. EPA because of their carcinogenicity (Carter 1974).

Chlordane, or 1,2,4,5,6,7,8,8-octachloro-3a,4,7,7a-tetrahydro-4,7-methanointhane, is chemically related to heptachlor except that the double bond has been chlorinated. The behavior of this insecticide in the model ecosystem clearly demonstrates its persistence and tendency to accumulate in the organisms of this system (Table 45). The water of the model ecosystem contained only 5.98 percent chlordane, but the alga, snail, mosquito, and fish contained 94.51, 91.17, 47.64, and 77.86 percent, respectively, of their radioactive materials as chlordane. The EM values for chlordane for the alga, snail, mosquito, and fish were 98,386, 132,613, 6,132, and 8,261, respectively. Clearly, the continued use of chlordane, along with its minor contaminant, heptachlor, will lead to problems of accumulation in food chains, which can lead to residues of these two pesticides in humans. Unpublished data accumulated by federal monitoring agencies have indicated that 95 percent of the adipose tissue taken from humans in the United States contains residues of heptachlor. Further, nearly 70 percent of U.S. poultry, fish, and dairy products contain residues of heptachlor. The data of this model-ecosystem experiment provide background information which explains the high incidence of heptachlor residues in humans and food.

FUNGICIDE TEST RESULTS

Captan, or *N*-trichloromethylthio-4-cyclohexene-1,2-dicarboximide, is the most versatile of the general foliar

fungicides for the treatment of fruits and vegetables. In the model ecosystem it was found to be extensively degraded, producing at least 15 degradation products in the water phase (Table 46). No intact captan was identified in any of the organisms of the system, and only trace amounts of degradation products were found. Captan appears not to offer any environmental problems following normal use.

Hexachlorobenzene has had some use as a fungicide in seed treatment, replacing in part the organomercurial fungicides. In the model system it was extremely persistent and substantially bioaccumulative, the parent compound comprising 85.1 percent of the total extractable radioactive materials in the alga, 87.2 percent in the daphnia, 58.3 percent in the mosquito, and 27.7 percent in the fish (Table 47) (Metcalf et al. 1973). EM values ranged from 144 to 1,248. The degradation of hexachlorobenzene occurs through hydrolysis to pentachlorophenol and other chlorophenols of increasing water solubility.

Hexachlorobenzene used as a fungicide on wheat caused an epidemic of thousands of cases of cutaneous porphyria in humans in Turkey (Schmid 1960), and the compound has been found in human tissues nearly everywhere, ranging up to 0.29 ppm in adipose tissues in Great Britain (Abbott et al. 1972). Hexachlorobenzene is clearly an undesirable environmental pollutant.

Pentachlorophenol is the fungicide in largest scale use in the United States as a timber and paper pulp preservative and mildewproofing. It is also used as a soil and timber poison against termites and as a nonselective herbicide. In the model ecosystem pentachlorophenol accumulated in the various organisms to a moderate degree (Table 48). EM values were 5–205. Pentachlorophenol constituted 15.1 percent of the total extractable radioactive materials in the alga, 12.2 percent in the snail, 33.3 percent in the mosquito,

55.5 percent in daphnia, and 51.2 percent in the fish. It is apparently degraded through a series of chlorinated phenols, and 10 degradation products were found in the water phase.

Pentachlorophenol, because of its high toxicity to nearly all forms of life as an oxidative phosphorylation uncoupler and its stability, can be a dangerous environmental pollutant. Its use as an herbicide in Japan has resulted in its presence in almost all Japanese river waters at concentrations of 0.01-0.1 ppb (Goto 1971).

DISCUSSION

The data shown in the preceding tables, illustrating the fates of a variety of pesticides in the laboratory model ecosystem, can be used for predictive purposes in a number of ways.

BIOLOGICAL EFFECTS

The dosages applied in the model ecosystem are realistic in terms of those used in the field, i.e., 0.2-1.0 pound per acre (0.22-1.1 kg per ha). Therefore, the biological results observed are meaningful as predictors of the environmental impact of the pesticide studied. The most dramatic results on nontarget species were found with the organochlorine insecticides endrin, dieldrin, and heptachlor epoxide. Endrin applied at the equivalent of 0.2 pound per acre (0.22 kg per ha) repeatedly killed all daphnia and mosquitoes in the system, and the necessity for restocking delayed the termination of the experiment to over 60 days. Fish added to the endrin system showed violent convulsions within 10-15 minutes and died within a few hours. Similar results were experienced with heptachlor epoxide, which killed daphnia and mosquitoes for 56 days after having been applied at 0.2 pound per acre (0.22 kg per ha). Dieldrin was highly toxic to daphnia and mosquitoes, which did not survive at any time during the experiment.

Temephos, the highly effective mosquito larvicide, killed mosquito larvae

so persistently that the experiment was prolonged to 53 days. Chlorpyrifos and methyl chlorpyrifos even at the 1.0-mg dosage were highly toxic to daphnia, and chlorpyrifos adversely affected algae.

The carbamate insecticides carbaryl and carbofuran were extremely toxic to daphnia in the initial stages of the experiments.

Some of the herbicides, especially metribuzin and bifenox, were highly toxic to algae in the model ecosystem. Surprisingly, the insecticide methoxychlor, or its degradation products, also affected algae adversely.

DEGRADATIVE PRODUCTS

This parameter is, of course, the direct measure of biodegradability. In general, the larger the number of degradative products in the water and in the organisms of the model ecosystem, the lower the degree of ecological magnification and the higher the amount of unextractable radioactive materials. Thus, DDE with two degradation products and DDT with four were the worst offenders in ecological magnification in contrast to temephos, carbaryl, and metribuzin, each with 11 degradative products, and chlordimeform with 13; each of the latter four compounds showed zero ecological magnification. Clearly, the relationship is not precise, because the variety of positions of radiolabeling limits the extent to which degradative products can be identified. Moreover, the formation of secondary toxicants, such as the epoxides, e.g., dieldrin from aldrin and heptachlor epoxide from heptachlor, provides products that are substantially more environmentally stable and ecologically magnified than are the parent compounds.

Nevertheless, knowledge of the key degradative products of any pesticide is important in characterizing its environmental impact. The model ecosystem not only provides useful information about the chemical nature of degradation products and about

degradative pathways, but also indicate potential rates and locations of storage and bioconcentration of pesticides and their degradation products. As examples, in addition to those of dieldrin and heptachlor epoxide, Banamite (Table 49) produced an unidentified degradation product, designated II, which was ecologically magnified 3,013-fold in fish and 19,824-fold in snails. Metrabuzin (Table 12) produced an unidentified product, designated II, which was ecologically magnified 175-fold in fish. Even the highly degradable malathion produced an unidentified product, designated III, which showed apparent ecological magnification of about 19,500-fold (Table 20).

ECOLOGICAL MAGNIFICATION

The accumulation of lipid-soluble, water-insoluble pesticides in living organisms is one of the most disturbing features of environmental pollution by

pesticides. The laboratory model ecosystem is particularly suitable for determining "ecological magnification," or the pesticide concentration in an organism divided by the pesticide concentration in the water. When ecological magnification is considered for the fish (*Gambusia*), we find that the values from the data in the tables vary from 0 to 10^5 . Such ecological magnification is a function of the partition coefficient in lipid/water and the stability of the pesticide and its metabolites in the animal. As shown in Fig. 2, an effective approximation is obtained when the water solubility of the pesticide in parts per billion (ppb) is plotted as a log function against ecological magnification. There is clearly an inverse relationship, with the least water-soluble pesticides accumulating to the highest degree. This relationship is highly significant, with a correlation coefficient of $r = -0.76$, and it is sub-

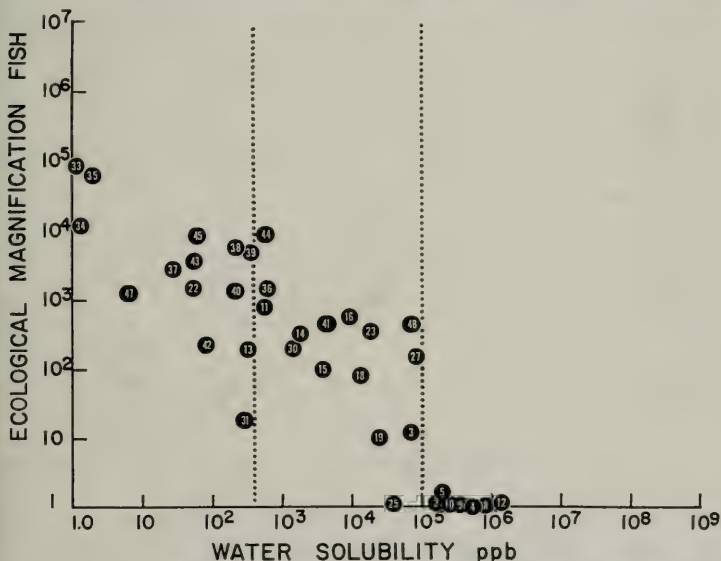


Fig. 2.—The relationship between the water solubility of pesticides, numbered as in Tables 2–49, and the ecological magnification of parent compounds in the mosquito fish in the laboratory model ecosystem. A highly significant correlation ($r = -0.76$) exists.

stantially predictable. Thus, it is of great importance to know the water solubility of even the least soluble compounds. From this information it is possible to make a reliable estimate of the potentialities of new pesticides to accumulate in the tissues of fish and other aquatic organisms. Our study suggests a classification of pesticides as:

1. water solubility < 0.5 ppm, *likely to be environmentally hazardous*
2. water solubility > 50 ppm, *likely to be environmentally nonhazardous*
3. water solubility from 0.5 to 50 ppm, *to be used with caution*

The lines of demarcation between the three classes obviously are not sharp, and the ultimate hazard also depends upon lipid partitioning, the rapidity of pesticide degradation in living animals, use patterns, and amounts applied. However, practical experience has already shown that most of the

pesticides with water solubilities of < 0.5 ppm demonstrate bioaccumulation following field use and that most of those with water solubilities of > 50 ppm have not shown bioaccumulation. The large group of pesticides with water solubilities between 0.5 and 50 ppm represent those which may demonstrate bioaccumulation under some conditions of use, e.g., in lakes or oceans with very cold water. Their use patterns should be judged accordingly.

UNEXTRACTABLE RADIOACTIVE MATERIALS

This parameter measures the conversion of the pesticide under investigation and its primary degradation products into simple degradation products which enter the metabolic pool of an organism and are resynthesized into normal tissue ingredients. The percentage of unextractable radioactive materials can be determined for many of the pesticides investigated by adding the amount of

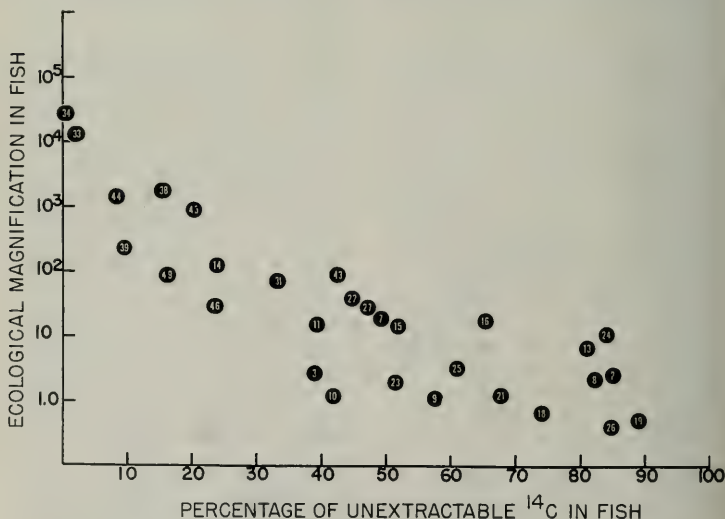


Fig. 3.—The relationship between the percentage of radioactive materials extractable from the mosquito fish of the laboratory model ecosystem and the total body accumulation of parent pesticide, numbered as in Tables 2-49, and all of its degradation products. There is a highly significant correlation ($r = -0.74$).

unextractable radioactive materials to the total extractable radioactive materials and determining the fraction. The values obtained in the fish (*Gambusia*), for example, range from 0.34 percent for DDE to about 90 percent for fenitrothion. As shown in Fig. 3, a highly significant correlation ($r = -0.74$) exists between the percentage of unextractable radioactive materials and the *in vivo* stability of the pesticide and its principal degradation products as measured by the total biomagnification of the radioactive materials from the water to the fish (or other organism).

Considering that two different

methods for determining amounts of unextractable radioactive materials were used, i.e., total combustion analysis and solubilization, the results are surprisingly predictable. Clearly, pesticides and their degradation products which are highly lipid soluble in the tissues of organisms are almost quantitatively extractable and leave small amounts of unextractable radioactive materials. As a tentative guideline we suggest that pesticides which produce 40 percent or more of unextractable radioactive materials in the fish in the model ecosystem evaluation will not be likely to cause serious problems with environmental quality.

Table 2.— R_t values and amounts, in parts per million, of alachlor^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ^{14}C		0.0457	0.0898	0.321	0.00	1.767	0.843	0.0452	0.125
I ^c	0.70	0.000948	...	...	...	...	...	...	...
Alachlor	0.61	0.00105	...	...	...	...	...	...	...
II	0.51	0.00344	...	...	...	...	...	...	...
III	0.43	0.0141	...	...	...	...	...	...	...
IV	0.33	0.00224	...	...	...	...	...	...	...
V	0.27	...	...	...	...	...	...	...	...
VI	0.20	0.00169	...	...	...	...	0.658	...	...
VII	0.13	0.00172	...	...	...	...	...	...	...
VIII	0.07	0.00369	...	...	...	...	...	...	...
Origin	0.00	0.00501	...	...	...	...	...	...	...
Unextractable ^{14}C		0.0118	0.569	0.524	0.422	2.961	0.544	0.244	0.106

^a2-chloro-2',6'-diethyl-N, N'-(methoxymethyl)-acetanilide, ^{14}C -ring UL.^bSilica Gel GF-254, methanol-benzene, 5:95 by volume.^cRoman numerals indicate compounds whose chemical structures are unknown.

Table 3.—R_t values and amounts, in parts per million, of atrazine^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.2281	2.7562	0.3779	0.5352	0.5916
Atrazine	0.43	0.03181	2.4059	0.2386	...	0.3511
A ^c	0.41	0.01575	0.2100	0.05479	...	0.07356
B ^d	0.38	0.005398	0.04934	0.02796	...	0.05496
I ^e	0.30	0.003681	...	...	...	...
II	0.25	0.001323	...	...	...	...
III	0.17	0.0008116	0.01792	...	...	0.03302
IV	0.11	0.001200	...	...	...	...
V	0.05	0.0004273	0.01020	0.02226	...	0.01462
Origin	0.00	0.002644	0.06284	0.03424	...	0.06436
Unextractable ¹⁴ C		0.1651	4.1907	0.04981	1.6726	0.2290

^a 2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine, ¹⁴C-ring UL.

^b Silica Gel GF-254, benzene; acetic acid; water, 50:50:3.

^c A = 2-amino-4-chloro-6-(isopropylamino)-s-triazine.

^d B = 2-amino-4-chloro-6-(ethylamino)-s-triazine.

^e Roman numerals indicate compounds whose chemical structures are unknown.

Table 4.—R_t values and amounts, in parts per million, of bentazon^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Uca</i> (crab)	<i>Corbicula</i> (clam)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.514	0.109	0.032	2.725	0.182	0.092	0.084	0.146	0.0120
A ^c	0.77	0.0207	...	...	0.622	...	...	...	...	...
B ^d	0.63	...	...	...	1.266	...	...	...	...	...
Bentazon	0.52	0.0505	...	...	0.510	...	...	...	...	...
Origin	0.00	0.00306	...	...	0.327	...	...	...	...	...
Unextractable ¹⁴ C		0.440	0.759	0.021	3.08	0.407	0.168	0.378	0.716	0.036

^a 3-isopropyl-1*H*-2,1,3-benzothiadiazin-4-(3*H*)-one-2,2-dioxide, ¹⁴C-ring UL.

^b Silica Gel GF-254, benzene-ethanol, 60:40 by volume.

^c A = N-isopropylanthranilamide.

^d B = Anthranilic acid.

Table 5.—R_t values and amounts, in parts per million, of cyanazine^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0322	0.129	0.311	0.0196	0.629	0.0454	0.0277	0.0354
Cyanazine	0.55	0.00321	...	...	...	0.621	...	...	...
A ^c	0.47	0.0107	...	0.172	...	...	...	...	...
B ^d	0.37	0.000142	...	...	...	...	...	...	...
C ^e	0.26	0.0000568	...	...	...	...	...	...	...
I ^f	0.16	0.0000768	...	...	...	...	...	...	...
II	0.07	0.0000868	...	0.0579	...	...	...	...	...
Origin	0.00	0.0000534	...	0.0812	...	0.00818	...	...	...
Unextractable ¹⁴ C		0.00357	0.127	0.209	0.0202	0.6253	0.0624	0.0751	0.0157

^a2-chloro-4-(1-cyano-1-methylethylamino)-6-ethylamino-s-triazine, ¹⁴C-ring UL.^bSilica Gel GF-254, methanol-acetone-chloroform, 5:45:50 by volume.^cA=2-chloro-4-amino-6-(1-methyl-1-cyanoethylamino)-s-triazine.^dB=2-chloro-4-ethylamino-6-(1-methyl-1-carboxamidoethylamino)-s-triazine.^eC=2-chloro-4-amino-6-(1-methyl-1-carboxamidoethylamino)-s-triazine.^fRoman numerals indicate compounds whose chemical structures are unknown.

Table 6.— R_t values and amounts, in parts per million, of dicamba^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea) (aquatic plant)	<i>Elodea</i> (snail)	<i>Physa</i> (mosquito)	<i>Culex</i> (fish)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.183	0.228	0.0128	0.743	0.000	0.325	0.0720	0.0736	0.00665
Dicamba	0.86	0.162	...	...	...	...	...	...	...	...
A ^c	0.38	0.0185	...	...	...	...	...	...	...	...
B ^d	0.04	0.000182	...	...	0.743	...	...	...	...	...
Unextractable ¹⁴ C		0.0022	1.390	0.0144	0.374	0.167	0.593	0.252	0.281	0.0122

^a 3,6-dichloro-o-anisic acid, ¹⁴C-ring UL.

^b Whatman No. 1 filter paper, benzene-acetic acid, 2:1 by volume.

^c A = 3,6-dichloro-5-hydroxy-2-methoxybenzoic acid.

^d B = Conjugated metabolite.

Table 7.— R_t values and amounts, in parts per million, of phenmedipham^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.028	4.22	2.69	1.312	0.545
Phenmedipham		...	...	...	...	...
A ^c	0.64	0.0102	...	...	...	...
B ^d		trace ^f	...	...	...	...
I ^e	0.99	...	0.067	0.497	0.131	...
II	0.96	...	0.131	0.153	0.101	...
III	0.76	...	0.139	...	...	...
IV	0.68	...	0.372	...	...	...
V	0.35	...	0.355	...	...	...
VI	0.18	...	0.506	...	...	...
Origin	0.00	0.0178	2.65	2.04	1.080	0.545
Unextractable ¹⁴ C		0.018	13.08	7.00	1.978	0.535

^a Methyl *m*-hydroxycarbanilate *m*-methylcarbanilate, ¹⁴C-ring UL.^b Silica Gel GF-254, diethyl ether:petroleum ether:chloroform, 6:3:1 by volume.^c A = *N*-(3-hydroxyphenyl)-methyl urethane.^d B = 3-methylaniline.^e Roman numerals indicate compounds whose chemical structures are unknown.^f Determined by gas chromatography.Table 8.— R_t values and amounts, in parts per million, of 2,4-D^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.2048	5.498	2.752	0.757	0.0454
I ^c	0.97	...	0.282	0.178	0.285	...
II	0.89	...	1.030	0.456	...	...
III	0.80	...	0.477	0.477	0.301	...
IV	0.65	...	0.377	...	...	...
V	0.58	0.0000641	0.295	...	...	0.0431
VI	0.63	0.00269	...	...	...	...
VII	0.56	0.00212	...	...	...	...
VIII	0.49	0.00226	...	...	...	...
IX	0.39	0.000417	...	...	...	...
X	0.10	0.000474	1.675	0.768	...	...
XI	0.067	0.000271	...	...	...	...
Origin	0.00	0.000185	1.362	0.873	0.171	0.00226
Unextractable ¹⁴ C		0.012	17.625	7.555	6.421	0.211

^a 2,4-dichlorophenoxyacetic acid, ¹⁴C-ring UL.^b Silica Gel GF-254, benzene-dioxane-acetic acid, 90:25:4 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.

Table 9.—R_z values and amounts, in parts per million, of propachlor^a and its degradation products found in the water and organisms of a model ecosystem.

	R _z ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00901	0.0211	0.00619	0.00930	0.00243	0.0749	0.0264	0.00605
I ^c	0.69	0.0000622	...	...	...	...	...	...	...
II	0.62	0.000169	...	...	...	...	...	...	...
Propachlor	0.55	0.0000564	...	...	...	...	...	...	...
III	0.40	0.00318	...	...	...	...	...	...	...
IV	0.30	...	...	...	...	...	...	...	...
V	0.27-0.15	0.000421	...	...	...	...	0.0154	...	...
VI	0.10	0.000272	...	...	...	...	...	...	...
VII	0.03	0.000319	...	...	...	...	...	...	...
Origin	0.00	0.000394	...	...	...	...	...	...	...
Unextractable ¹⁴ C		0.00414	0.186	0.00886	0.0476	0.0869	0.177	0.134	0.00854

^a 2-chloro-N-isopropylacetanilide, ¹⁴C-ring UL.

^b Silica Gel GF-254, methanol-benzene, 5:95 by volume.

^c Roman numerals indicate compounds whose chemical structures are unknown.

Table 10.— R_t values and amounts, in parts per million, of pyrazon^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0321	0.0758	0.0498	0.499	0.0536	0.105	0.127	0.175	0.0336
Pyrazon	0.63-0.69	0.0212	...	...	0.476	...	...	...	...	...
A ^c	0.47-0.51	0.0000714	...	...	...	...	...	...	...	...
I ^d	0.40-0.43	0.0000430	...	...	...	...	...	...	...	...
II	0.23	0.0000260	...	...	...	...	...	...	...	...
III	0.16	0.0000471	...	...	...	...	...	...	...	...
IV	0.10	0.0000764	...	...	...	...	...	...	...	...
Origin	0.00	0.000136	...	...	0.0233	...	...	...	...	...
Unextractable ¹⁴ C		0.0105	0.131	0.018	0.130	0.0455	0.0552	0.0592	0.148	0.0237

^a 5-amino-4-chloro-2-phenyl-3-(2H)-pyridazinone, ¹⁴C-phenyl ring.^b Silica Gel GF-254, benzene-ethanol, 60:40 by volume.^c A = 5-amino-4-chloro-3(2H)pyridazinone.^d Roman numerals indicate compounds whose chemical structures are unknown.

Table 11.—R_f values and amounts, in parts per million, of trifluralin^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Daphnia</i> (water flea)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0489	0.445	6.663	0.238	0.767
Trifluralin	0.74	0.000282	...	5.046	...	0.261
I ^c	0.51	0.000066	...	...	...	...
A ^d	0.39	0.000087	...	0.337	...	...
B ^e	0.32	0.000374	...	...	...	...
II	0.24	0.000322	...	0.0399	...	...
III	0.20	0.000139	...	0.216	...	...
IV	0.17	0.000514	...	...	...	...
C ^f	0.13	0.000803	...	...	...	...
V	0.11	0.000686	...	...	...	...
VI	0.07	0.00141	...	0.228	...	...
VII	0.04	0.00203	...	...	...	...
Origin	0.00	0.0169	...	0.796	...	0.506
Unextractable ¹⁴ C		0.0253	1.017	6.648	0.520	1.011

^a *a,a,a*-trifluoro-2,6-dinitro-*N*, *N*-dipropyl-*p*-toluidine, ¹⁴C-ring UL.^b Silica Gel GF-254, hexane-acetone-methanol, 90:10:2 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = *a,a,a*-trifluoro-2,6-dinitro-*N*-propyl-*p*-toluidine.^e B = 2,6-dinitro-4-trifluoromethyl aniline.^f C = 2-ethyl-5-trifluoromethyl-7-nitrobenzimidazole.Table 12.—R_f values and amounts, in parts per million, of metribuzin^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.6524	1.2880	1.559	1.342
I ^c	0.87	0.2911	0.762	1.307	0.307
II	0.83	0.003118	0.3920	...	0.546
A ^d	0.57	0.008965	...	...	0.291
III	0.35	0.1292	...	...	...
IV	0.32	0.006435	...	...	...
B ^e , C ^f	0.24	0.09676	...	...	0.0746
V	0.20	0.0005374	...	...	...
VI	0.17	0.001252	...	...	...
VII	0.12	0.005675	...	...	...
VIII	0.09	0.001158	...	...	...
IX	0.06	0.00005275	...	...	...
X	0.04	0.0005046	...	...	...
XI	0.01	0.002047	0.05217	0.05158	0.0140
Origin	0.00	0.005278	0.05217	0.2407	0.0769
Unextractable ¹⁴ C		0.1003	0.4578	3.7546	0.3498

^a 4-amino-6-*tert*-butyl-3-(methylthio)-*as*-triazin-5(4*H*)-one 5-¹⁴C.^b Chloroform: acetone, 9:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = Desamino metribuzin.^e B = Desmercapto metribuzin.^f C = Desamino desmercapto metribuzin.

Table 13.— R_f values and amounts, in parts per million, of bifenox^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0376	3.267	1.650	0.290	0.211
I ^c	0.82	0.000108	...	...	0.071	...
Bifenox	0.73	0.000745	3.189	1.203	0.219	0.156
A ^d	0.66	0.000125	...	0.256	...	...
II	0.60	0.000092	...	...	...	...
III	0.45	0.000125	...	...	...	...
B ^e	0.33	0.000325	...	0.088	...	0.020
Origin	0.00	0.0301	0.78	0.103	trace	0.026
Unextractable ¹⁴ C		0.0061				

^a Methyl-5-(2',4'-dichlorophenoxy)-2-nitrobenzoate, ¹⁴C nitrophenyl ring UL.^b Silica Gel GF-254, benzene:dioxane:acetic acid, 90:30:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = Methyl-5-(2',4'-dichlorophenoxy)-2-amino benzoate.^e 2,4-dichlorophenoxy-2-nitro-5-benzoic acid.Table 14.— R_f values and amounts, in parts per million, of chlorpyrifos^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00056	0.0261	0.158	0.063	0.0711
Chlorpyrifos	0.76	0.00011	0.0079	0.076	0.005	0.0352
A ^c	0.60	...	...	...	...	...
B ^d	0.60	0.000115	0.0051	0.051	0.022	0.0207
Origin	0.00	0.00005	0.0131	0.031	0.036	0.0152
Unextractable ¹⁴ C		0.00028	0.1507	0.0456	...	0.0223

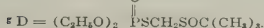
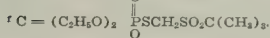
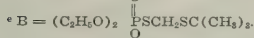
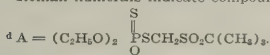
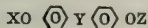
^a O,O-diethyl-O-(3,5,6-trichloro-2-pyridyl)-phosphorothionate, ¹⁴C-ring UL.^b Silica Gel GF-254, benzene:dioxane:acetic acid, 90:15:1 by volume. Pyridinol (R_f = 0.17) and P = O ester (R_f = 0.90) separated with solvent system, acetonitrile:hexane:acetone:NH₄OH 70:10:15:5, by volume.^c A = Chlorpyrifosoxon.^d B = 3,5,6-trichloro-2-pyridol.Table 15.— R_f values and amounts, in parts per million, of chlorpyrifos-methyl^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00262	0.0780	0.0882	0.220	0.0367
Chlorpyrifos-methyl	0.75	0.00008	0.0382	0.0435	0.15	0.0076
A ^c	0.54	...	...	...	...	...
B ^d	0.60	0.0002	0.0087	0.0082	0.037	0.0109
Origin	0.00	0.00154	0.0051	0.0067	0.033	0.0101
Unextractable ¹⁴ C		0.0009	0.4703	0.2110	...	0.0398

^a O,O-diethyl-O-(3,5,6-trichloropyridinyl) phosphorothionate, ¹⁴C-ring UL.^b Silica Gel GF-254, benzene: dioxane:acetic acid, 90:15:1 by volume. Pyridinol (R_f = 0.17) and P = O ester (R_f = 0.83) separated by solvent system, acetonitrile:hexane:acetone:NH₄OH, 70:10:15:5, by volume.^c A = Chlorpyrifosoxon methyl.^d B = 3,5,6-trichloro-2-pyridol.

Table 16.— R_f values and amounts, in parts per million, of Counter®¹ and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00259	0.1063	0.1556	0.1517	0.0427
I ^c	0.83	...	...	...	0.1156	...
Counter®	0.77	0.00002	0.0035	0.0366	0.0072	0.0107
A ^d	0.66	0.00006	...	...	...	...
B ^e	0.54	0.000062	trace	0.0241	...	...
C ^f	0.40	0.000357	...	...	...	...
II	0.29	0.000046	0.0071	...	...	...
III	0.18	0.000018	...	...	...	...
D ^g	0.13	0.000017	0.0106	...	...	trace
IV	0.03	0.000007	0.0213	...	...	...
Origin	0.00	0.000283	0.0638	0.0494	0.0289	0.0320
Unextractable ¹⁴ C		0.00174	0.8913	0.778	0.4282	0.0813

^a O,O-diethyl S-(tert-butylthio)-methyl phosphorodithioate, ¹⁴C-tert-butyl.^b Silica Gel GF-254, benzene:acetone, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 17.— R_f values and amounts, in parts per million, of temephos¹ and its degradation products found in the water and organisms of a model ecosystem.

X	Y	Z	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Gambusia</i> (fish)
Total 3H				0.000280	0.00991	0.09161	0.00099
(MeO) ₂ P=S	S	(MeO) ₂ P=S		0.0000013	0.00195	0.01876	...
(MeO) ₂ P=S	SO	(MeO) ₂ P=S		0.000002	0.00066	0.01483	...
(MeO) ₂ P=S	SO ₂	(MeO) ₂ P=S		0.0000007	0.00078	0.00396	...
(MeO) ₂ P=O	S	(MeO) ₂ P=O		0.00000014	0.00127	0.00785	...
(MeO) ₂ P=O	SO ₂	(MeO) ₂ P=O		...	0.00066	...	...
(MeO) ₂ P=S	SO ₂	(MeO) ₂ P=O		...	0.00040	0.00698	...
(MeO) ₂ P=S	S	(MeO) ₂ P=O		trace	0.00066	0.02705	...
(MeO) ₂ P=S	SO ₂	H		0.000002	0.00036	...	...
(MeO) ₂ P=S	S	H		0.000002	0.00129	...	...
H	S	H		0.000001	0.00045	...	...
H	SO ₂	H		0.0000024	0.00046	0.00175	...
(MeO) ₂ P=O	S	H		0.000008	0.00064	0.01178	...
Origin				0.00019	0.00033	0.00436	...
Unextractable ¹⁴ C				0.000070	...	...	...

^a O,O-dimethylphosphorothioate ester of 4,4' dihydroxydiphenyl sulfide, ³H-ring-labeled.^b Silica Gel GF-254 three dimensional TLC: 1.toluene. 2.methanol:chloroform:toluene, 10:95:95 by volume. 3.nitromethane:acetonitrile, 25:65:110 by volume.

Table 18.— R_t values and amounts, in parts per million, of fonofos^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.1079	0.2977	0.2831	0.6863	0.08500
Fonofos	0.92	0.0008866	0.09556	0.07635	0.6133	0.06845
I ^c	0.76	0.0000653	0.02203	...	...	...
II	0.68	0.0002602	...	...	...	...
III	0.62	0.001504	0.07905	...	...	...
IV	0.37	0.002806	0.01887	...	...	...
V	0.29	0.0005997	...	...	...	...
VI	0.22	0.0008081	...	...	...	...
VII	0.19	0.0001472	...	...	...	...
VIII	0.13	0.0003656	...	...	...	...
IX	0.10	0.0001383	0.0401	...	...	...
X	0.09	0.0000765	...	...	...	...
XI	0.08	0.0002311	...	0.08748	...	0.01193
XII	0.04	0.0005152	0.01494	...	...	...
Origin	0.00	0.008277	0.02712	0.1193	0.07302	0.004624
Unextractable ¹⁴ C		0.09126	0.5247	2.2550	5.8578	0.2453

^a O-ethyl, S-phenyl ethylphosphonodithioate, ¹⁴C-O-ethyl.^b Silica Gel GF-254, chloroform:ethyl acetate, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 19.— R_t values and amounts, in parts per million, of fenitrothion^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ³² P		0.1136	2.5579	5.270	0.0829	0.0545
I ^c	0.92	0.00238	...	...	...	...
Fenitrothion	0.81	0.00247	0.8632	...	0.0055	0.0242
II	0.73	0.00004	...	...	...	...
A ^d	0.52	0.00088	...	...	...	0.0057
III	0.22	0.00030	...	...	...	...
IV	0.13	0.00338	...	...	...	...
V	0.06	0.00030	...	...	...	...
Origin	0.00	0.02438	1.2947	5.2700	0.0774	0.0246
Unextractable ¹⁴ C		0.07949	10.5993	1.5802	1.0983	8.9550

^a O,O-dimethyl O-(3-methyl-4-nitrophenyl) phosphorothionate, ³²P.^b Silica Gel GF-254, hexane (Skellysolve B):ether, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = Fenitroxon or dimethyl 3-methyl-4-nitrophenyl phosphate.

Table 20.— R_t values and amounts, in parts per million, of malathion^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ^{14}C		0.01659	0.421	0.577	6.97	1.43
I ^c	0.81	...	0.319	...	1.82	...
II	0.75	0.0000447	...	0.338	...	0.119
III	0.63–0.67	0.0000335	...	...	2.34	0.655
IV	0.50	0.0000546	...	...	0.947	0.1033
V	0.36	0.0000784	...	...	0.299	...
VI	0.31	...	...	...	...	0.0254
VII	0.15	0.0000345	...	...	...	0.0737
VIII	0.05	0.0000754	...	...	0.275	0.0342
Origin	0.00	0.003868	0.102	0.139	1.283	0.420
Unextractable ^{14}C		0.0124	...	...	...	...

^a *O,O*-dimethyl-*S*-(1,2-dicarboethoxyethyl)-phosphorodithioate, ^{14}C -*O,O*-methyl.^b Silica Gel GF-254, benzene:acetic acid, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.

Table 21.— R_t values and amounts, in parts per million, of acephate^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0245	1.043	0.100	2.285	0.403	0.417	0.926	0.822	0.0309
I ^c	0.93	0.000477	0.936	...	2.038	0.257	0.407	0.796	0.797	...
A ^d	0.79	0.000124	...	...	...	...	...	...	...	...
Acephate	0.70	0.000282	...	...	...	...	...	...	...	...
B ^e	0.45	...	...	...	...	...	...	...	...	...
C ^f	0.33	0.0000150	...	...	...	...	...	...	...	...
II	0.25	...	0.0538	...	...	...	...	...	...	...
III	0.11	...	0.0142	...	...	0.00280	...	...	...	...
Origin	0.00	0.0000255	0.0395	...	0.247	0.143	0.0098	0.130	0.0247	...
Unextractable ¹⁴ C		0.0236	1.043	0.148	3.631	1.979	1.435	2.769	2.466	0.0621

^a O-methyl-S-methyl-N-acetylphosphoramidothioate, ¹⁴C-S-methyl.^b Silica Gel GF-254, alumina plate 15% acetic acid in benzene:propanol, 1:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = O,S-dimethyl phosphoramidothioate.^e B = O,S-dimethyl phosphorothioic acid-sodium salt.^f C = S-methyl N-acetyl phosphoramidothioate.

Table 22.— R_t values and amounts, in parts per million, of leptophos^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.180	31.637	53.696	1.866
Leptophos	0.93	0.00108	13.221	52.270	1.559
I ^c	0.85	...	15.753	...	...
II	0.25	...	...	0.105	0.0313
III	0.24	...	...	...	0.0235
IV	0.22	...	...	0.128	...
V	0.20	...	2.357	...	...
VI	0.13	0.002712	...	...	...
VII	0.12	0.00647	...	...	...
VIII	0.10	0.000199	...	...	...
IX	0.09	0.00392	...	...	...
X	0.07	0.0000691	...	...	...
XI	0.05	0.009094	0.009	...	...
XII	0.03	0.000147	...	...	0.0235
Origin	0.00	0.02170	0.297	1.193	0.199
Unextractable ¹⁴ C		0.1351	57.241	11.612	1.555

^a *O*-(4-bromo-2,5-dichlorophenyl)-*O*-methyl phenylphosphonothionate, ¹⁴C-*O*-methyl.^b Silica Gel GF-254, benzene:chloroform, 1:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 23.— R_t values and amounts, in parts per million, of parathion^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Oedogonium</i> (alga)	<i>Daphnia</i> (water flea)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.003	0.3969	0.2987	0.2701	0.2031	0.1935
I ^c	0.97	0.000200	0.0356	...	...	...	...
Parathion	0.90	0.00030	...	...	...	...	0.1006
II	0.73	0.000060	...	...	...	...	...
A ^d	0.55	0.000136	...	...	...	...	0.0086
III	0.33	0.00025	...	...	...	...	0.0222
B ^e	0.25	0.0047	...	...	...	...	...
IV	0.13	0.00049	...	...	...	...	...
V	0.09	0.00274	...	...	...	...	...
Origin	0.00	0.00599	0.3613	0.2987	0.2701	0.2031	0.0621
Unextractable ¹⁴ C		0.0854	2.6284	0.3126	0.5818	0.4685	0.2055

^a *O,O*-diethyl *O*-4-nitrophenyl phosphorothionate, ¹⁴C-ring-2,6.^b Silica Gel GF-254, ether-hexane, 7:3 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = *p*-nitrophenol.^e B = Paraoxon.

Table 24.— R_t values and amounts, in parts per million, of metalkamate^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> ^c (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.003966	1.781	0.0206	0.287	0.128	0.945	0.119	0.178	0.0449
Metalkamate	0.98	0.0009539	0.980	...	0.0498	...	0.245	...	...	...
I ^d	0.95-0.62	0.000814	0.474	...	0.168	...	0.107	...	...	...
II	0.62-0.28	0.0000151	0.252	...	0.056	...	0.206	...	...	...
III	0.28-0.02	0.0000589	0.074	...	0.0079	...	0.119	...	...	...
Origin	0.00	0.0001031	0.00111	...	0.00508	...	0.268	...	...	...
Unextractable ¹⁴ C		0.00288	7.825	0.0826	1.590	1.420	1.510	0.662	0.602	0.230

^a 3:1 mixture of *m*-(1-ethylpropyl)-phenyl and *m*-(1-methylbutyl)-phenyl *N*-methylcarbamates, ¹⁴C-carbonyl labeled.^b Microfiber absorbent sheets impregnated with silica gel, acetone-*n*-hexane, 15:85 by volume.^c Clam died 7 days after the application of metalkamate to the system.^d Roman numerals indicate compounds whose chemical structures are unknown.

Table 25.—R_t values and amounts, in parts per million, of carbaryl^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea) (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.374	0.789	0.286	0.384	0.295	1.051	0.360	0.121
I ^c	0.95	...	0.175	...	0.118	...	0.057	...	0.03
II	0.87	0.000161	...	...	...	...	...	...	...
III	0.83	0.000155	...	...	...	...	...	...	...
A ^d	0.79	...	...	...	...	...	...	...	...
IV	0.67	0.000221	...	...	...	...	...	...	...
V	0.53	0.00006	...	...	...	...	...	...	...
VI	0.47	0.000133	...	...	...	...	...	...	...
B ^e	0.35	0.000081	...	...	...	...	...	...	...
C ^f	0.30	...	...	...	...	...	...	...	...
D ^g	0.26	...	...	...	...	...	...	...	...
VII	0.22	0.000018	...	...	...	...	...	...	...
E ^h	0.18	0.000099	...	...	...	...	...	...	...
VIII	0.12	0.000765	...	...	0.0095	...	0.085	...	...
IX	0.08	0.00151	...	...	...	...	...	...	...
Origin	0.00	0.00748	0.614	...	0.257	...	0.909	...	0.091
Unextractable ¹⁴ C		0.0267	3.964	1.341	0.738	2.385	3.511	2.657	0.337

^a 1-naphthyl N-methylcarbamate, ¹⁴C-ring UL.

^b Silica Gel GF-254 chloroform:methanol, 49:1 by volume.

^c Roman numerals indicate compounds whose chemical structures are unknown.

^d A = 1-naphthol.

^e B = 1-naphthyl-N-hydroxymethylcarbamate.

^f C = 5-hydroxy-1-naphthyl-N-methylcarbamate.

^g D = 4-hydroxy-1-naphthyl-N-methylcarbamate.

^h E = 7-hydroxy-1-naphthyl-N-methylcarbamate.

Table 26.—R_t values and amounts, in parts per million, of carbofuran^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (water plant)	(frog)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.115	0.815	1.087	1.089	2.697	0.502	1.645	1.071	0.0725
I ^c	0.98	0.001048	...	...	...	...	0.197	0.567	0.418	0.0462
A ^d	0.83	0.02978	...	0.0130	...	...	...	0.377	...	0.000304
B ^e and carbofuran	0.76	0.003889	...	...	...	...	...	...	...	...
C ^f	0.70	0.0005148	...	...	...	...	...	...	...	...
D ^g	0.60	0.0003728	...	...	...	...	...	...	...	...
E ^h	0.53	0.0003665	...	...	...	...	...	...	...	...
F ⁱ	0.46	0.0006071	...	...	...	...	...	...	...	0.00526
II	0.36	0.0007283	...	...	...	...	...	...	...	0.000828
III	0.28	0.001737	...	0.191	...	...	...	...	...	...
IV	0.13	0.003218	...	...	...	...	...	...	...	...
V	0.06	0.003328	...	...	...	...	...	...	...	...
Origin	0.00	0.017213	...	0.883	...	...	0.305	0.890	0.552	0.0216
Unextractable ¹⁴ C		0.0666	4.648	0.368	4.690	2.993	1.034	6.270	4.835	0.413

^a 2,2-dimethyl-2,3-dihydrobenzofuranyl-7-N-methylcarbamate, ¹⁴C-ring UL.^b Microfiber absorbent sheets impregnated with Silica Gel, acetone: n-hexane, 15:85 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = 7-hydroxy-2,2-dimethyldihydrobenzofuran.^e B = 3-keto-7-hydroxy-2,2-dimethyldihydrobenzofuran.^f C = 2,2-dimethyl-3-oxo-7-N-methylcarbamoyloxydihydrobenzofuran.^g D = 3,7-dihydroxy 2,2-dimethyldihydrobenzofuran.^h E = 2,2-dimethyl-7-N-hydroxymethylcarbamoyloxydihydrobenzofuran.ⁱ F = 2,2-dimethyl-3-hydroxy-7-N-methylcarbamoyloxydihydrobenzofuran.

Table 27.— R_f values and amounts, in parts per million, of propoxur^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00408	0.4617	0.3946	2.2913	0.1173
I ^c	0.92	...	0.2150	0.1330	0.4312	...
A ^d	0.74	0.000083	...	0.0406	...	0.0252
Propoxur	0.64	0.00032	0.0360	0.0928	0.4441	0.0468
B ^e	0.50	0.000032	...	0.0236	...	...
II	0.38	0.00001	...	...	...	...
C ^f	0.22	0.000006	0.0249	...	1.1520	0.0180
III	0.10	0.00001	...	0.0300	...	...
IV	0.08	0.000012	0.0598	...	...	...
Origin	0.00	0.00106	0.1260	0.0746	0.2640	0.0273
Unextractable ¹⁴ C		0.00255	3.9357	6.1600	21.900	0.1053

^a 2-isopropoxyphenyl *N*-methylcarbamate, ¹⁴C-2-isopropoxy.^b Silica Gel GF-254, chloroform:acetonitrile, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = 2-isopropoxyphenol.^e B = 2-isopropoxyphenyl carbamate.^f C = 2-isopropoxyphenyl *N*-hydroxymethyl carbamate.Table 28.— R_f values and amounts, in parts per million, of aldicarb^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Culex</i> (mos- quito)	<i>Gam- busia</i> (fish)
Total ¹⁴ C		0.16	17.0	2.32
Aldicarb ^c	0.54	0.031	16.7	1.31
A ^d	0.42	trace	...	1.01
B ^e	0.28	0.04	...	...
C ^f	0.14	0.056	...	...
Origin	0.00	0.025	0.3	...

^a 2-methyl-2-methylthiopropionaldoxymyl *N*-methylcarbamate, ¹⁴C-*tert*-carbon.^b Silica Gel GF-254, hexane: benzene: ethanol, 2:2:1 by volume.^c $\text{CH}_3\text{SC}(\text{CH}_3)_2\text{CH}=\text{NOC}(\text{O})\text{NHCH}_3$.^d A = $\text{CH}_3\text{SO}_2\text{C}(\text{CH}_3)_2\text{CH}=\text{NOH}$.^e B = $\text{CH}_3\text{SO}_2\text{C}(\text{CH}_3)_2\text{CH}=\text{NOC}(\text{O})\text{NHCH}_3$.^f C = $\text{CH}_3\text{SOC}(\text{CH}_3)_2\text{CH}=\text{NOC}(\text{O})\text{NHCH}_3$.

Table 29.— R_f values and amounts, in parts per million, of formetanate^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.11	44.98	2.10	1.61	1.17
I ^c	0.81	...	...	1.53	1.07	...
II	0.75	...	2.25	...	...	...
III	0.62	...	...	0.32	...	...
A ^d	0.35	0.0666	...	...	...	...
IV	0.27	...	2.70	...	...	...
V	0.14	...	4.05	...	...	...
Origin	0.00	0.0118	35.98	0.25	0.54	1.17
Unextractable ¹⁴ C		0.0316	22.10	9.02	5.59	1.71

^a 3-dimethylaminomethyleneiminophenyl *N*-methylcarbamate•hydrochloride, ¹⁴C-ring labeled.^b Silica Gel GF-254, ethyl acetate.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = *N*-formyl-3-aminophenol.Table 30.— R_f values and amounts, in parts per million, of methoprene^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00556	4.626	4.885	0.070
I ^c	0.83	...	0.0990	0.1924	...
Methoprene ^d	0.76	0.000086	2.220	1.500	0.0176
II	0.66	...	0.963	0.376	0.0305
A ^e	0.60	...	...	1.5490	...
B ^f	0.53	...	0.723	0.469	0.0181
C ^g	0.47	0.000075	...	0.0845	0.0017
Other		0.00024	0.332	0.500	
Origin	0.00	0.000576	0.289	0.45	0.0021
Unextractable ¹⁴ C		0.00458	...	...	...

^a Isopropyl-11-methoxy-3,7,11-trimethyldodeca-2,4-dienoate.^b Silica Gel GF-254, benzene:ethyl acetate:acetic acid, 100:50:5 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d Isopropyl-11-methoxy-3,7,11-trimethyldodeca-2,4-dienoate (5-¹⁴C).^e A = 11-methoxy-3,7,11-trimethyldodeca-2,4-dienoic acid.^f B = Isopropyl 11-hydroxy-3,7,11-trimethyldodeca-2,4-dienoate.^g C = 11-hydroxy-3,7,11-trimethyldodeca-2,4-dienoic acid.

Table 31.—R_t values and amounts, in parts per million, of dimilin^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^d	Difluorobenzoyl ^b Equivalents				Chlorophenyl Urea Equivalents ^c					
		Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.02356	1.0311	0.6670	5.2455	1.644	0.06909	0.6548	2.2306	13.3614	6.0701
I ^e	0.90	...	0.4028	...	0.7201	...	...	...	...	...	...
A ^f	0.83	...	...	...	...	...	0.0034	0.0778	...	...	...
II	0.77	0.00025	...	...	...	...	...	...	...	...	...
Dimilin	0.70	0.0057	0.4748	0.4891	4.4225	0.1097	0.0220	0.4019	2.0979	13.1369	0.3193
III	0.60	...	...	...	...	...	trace	...	...	...	...
B ^g	0.52	0.0018	...	...	...	0.1644	...	...	...	...	...
C ^h	0.50	...	...	...	...	...	0.0078	0.0389	...	...	0.3193
D ⁱ	0.45	0.00031	...	...	...	...	...	...	...	...	...
V	0.43	...	...	...	...	...	0.00055	...	...	...	...
VI	0.38	0.00020	...	...	...	...	...	...	...	...	...
VII	0.36	...	...	...	...	...	0.00061	...	...	...	...
E ^j	0.33	...	...	...	...	...	0.00056	...	...	...	...
VIII	0.26	...	...	...	...	...	0.00022	...	...	...	0.0297
IX	0.20	...	...	...	...	...	0.00015	...	...	...	...
F ^k	0.12	...	...	...	...	...	0.0072	0.0227	...	...	...
Origin	0.00	0.0060	0.1535	0.1779	0.1028	1.3703	0.0078	0.1135	0.1327	0.0174	5.2755
Unextractable ¹⁴ C		0.0093	4.9559	1.6210	1.9340	0.8227	0.0188	0.5726	0.2713	0.3436	0.8469

^a1-(2,6-difluorobenzoyl)-3-(4-chlorophenyl) urea.^b¹⁴C-label in 2,6-benzoyl moiety.^c¹⁴C-label in 4-chloroaniline moiety.^dSilica Gel GF-254 benzene:dioxane:acetic acid, 90:30:1 by volume.^eRoman numerals indicate compounds whose chemical structures are unknown.^fA=N,N-methyl-4-chloroaniline.^gB=2,6-difluorobenzoic acid.^hC=4-chloroaniline.ⁱD=2,6-difluorobenzamide.^jE=4-chloroacetanilide.^kF=4-chlorophenyl urea.

Table 32.— R_t values and amounts, in parts per million, of chlordimeform^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b		Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C	1	2	0.0427	0.9253	1.7682	0.3626	0.5259
Chlordimeform	0.00, 0.65	...	...	...	0.0710	...	...
A ^c	0.33, 0.09	0.00075	...	...	...	...	...
B ^d	0.43, 0.00	0.00179	...	...	...	...	...
C ^e	0.53, 0.35	0.00016	...	...	...	...	...
D ^f	0.10, 0.00	0.00085	0.109	...	...	...	...
E ^g	0.77, 0.71	0.00041	0.0933	0.255	...	0.0553	...
I ^h	0.83, 0.00	0.00052	0.181 ⁱ	...	...	...	...
II	0.83, 0.66	0.00031	...	...	...	...	...
III	0.73, 0.70	0.00026	...	...	...	...	...
IV	0.57, 0.90	...	...	...	...	0.0246	...
V	0.53, 0.03	0.00070	...	...	...	...	...
VI	0.52, 0.27	0.000077	...	...	...	...	...
VII	0.50, 0.23	0.00017	...	...	...	...	...
VIII	0.33, 0.23	0.00025	...	...	...	...	...
IX	0.23, 0.00	0.00077	...	...	...	...	...
Origin	0.00, 0.00	0.0125	0.542	1.442	...	0.446	...
Unextractable ¹⁴ C		0.0233	...	...	...	...	...

^a *N'*-(4-chloro-*o*-tolyl)-*N,N*-dimethylformamide, ¹⁴C-tolyl.^b Silica Gel GF-254 two dimensional tic: 1. benzene:dioxane:acetic acid, 90:30:1 by volume.

2. benzene:diethylamine, 95:5 by volume.

^c A = 2-methyl-4-chloroformanilide.^d B = 5-chloroanthranilic acid.^e C = 2-methyl-4-chloroaniline.^f D = 2-carboxy-4-chloroformanilide.^g E = 2,2'-dimethyl-4,4'-dichloroazobenzene.^h Roman numerals indicate compounds whose chemical structures are unknown.ⁱ Alga contained traces of unknowns totaling 0.181 ppm.Table 33.— R_t values and amounts, in parts per million, of DDT^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Physa</i> (snail)	<i>Culex</i> ^c (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.004	22.9	8.9	54.2
DDE	0.53	0.00026	12.0	5.2	29.2
DDT	0.34	0.00022	7.6	1.8	18.6
DDD	0.17	0.00012	1.6	0.4	5.3
Origin	0.00	0.0032	0.98	1.5	0.85

^a 2,2-bis-(*p*-chlorophenyl)-1,1,1-trichloroethane, ¹⁴C-ring UL.^b Silica Gel GF-254, petroleum ether solvent, b.p. 60–80°C.^c Dry weight.Table 34.— R_t values and amounts, in parts per million, of DDE^a and its degradation products found in the water and organisms of a model ecosystem.

	R_t^b	Water	<i>Physa</i> (snail)	<i>Culex</i> ^c (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.008	121.6	168.9	149.8
DDE	0.53	0.0053	103.5	159.5	145.0
Origin	0.0	0.0027	18.1	9.4	4.8

^a 2,2-bis-(*p*-chlorophenyl)-1,1-dichloroethylene, ¹⁴C-ring UL.^b Silica Gel GF-254, petroleum ether solvent, b.p. 60–80°C.^c Dry weight.

Table 35.—R_f values and amounts, in parts per million, of DDD^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.006	5.65	5.85	39.12
A ^c	0.53	...	0.24	...	2.08
I ^d	0.47	...	0.14	...	1.54
DDD	0.17	0.0004	3.3	3.43	33.4
II	0.05	...	0.87	...	...
Origin	0.00	0.0056	1.1	...	2.0

^a 2,2-bis-(*p*-chlorophenyl)-1,1-dichloroethane, ¹⁴C-ring UL.
^b Silica Gel GF-254, hexane (Skellysolve B).
^c A = ClC₆H₄C = CCl₂C₆H₄Cl.
^d Roman numerals indicate compounds whose chemical structures are unknown.

Table 36.—R_f values and amounts, in parts per million, of methoxychlor^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Physa</i> (snail)	<i>Culex</i> ^c (mosquito)	<i>Gambusia</i> (fish)
Total ³ H		0.0016	15.7	0.48	0.33
A ^d	0.32	...	0.7	...	...
Methoxychlor	0.25	0.00011	13.2	...	0.17
B ^e	0.07	0.00013	1.0	...	trace
C ^f	0.00	0.00003	trace	...	trace
D ^g	0.00	0.00003	...	...	...
Unknowns	trace	0.00009	trace	...	trace
Origin	0.00	0.00125	0.8	...	0.16

^a 2,2-bis-(*p*-methoxyphenyl)-1,1,1-trichloroethane, ³H-ring labeled.
^b Silica Gel GF-254, petroleum ether solvent, b.p. 60–80°C.
^c Dry weight.
^d A = CH₃OC₆H₄C = CCl₂C₆H₄OCH₃.
^e B = CH₃OC₆H₄HCCl₃C₆H₄OH.
^f C = HOC₆H₄HCCl₃C₆H₄OH.
^g D = HOC₆H₄C = CCl₂C₆H₄OH.

Table 37.—R_f values and amounts, in parts per million, of aldrin^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0117	19.70	57.20	1.13	29.21
Aldrin	0.81	0.00005	1.95	2.23	...	0.157
Dieldrin	0.71	0.0047	16.88	52.40	1.10	28.00
I ^c	0.63	...	0.57	2.05	...	0.612
A ^d	0.45	0.00052	0.12	0.17	...	0.322
B ^e	0.34	0.0004	0.079	0.217	...	0.088
C ^f	0.08	0.00039	0.015	...	...	...
Origin	0.00	0.0040	0.015	0.097	...	0.004
Unextractable ¹⁴ C		0.00155	...	...	...	...

^a 1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1,4-*endo*, *exo*-5,8-dimethanonaphthalene, ¹⁴C-ring.
^b Silica Gel GF-254, *n*-hexane:diethyl ether, 1:1 by volume.
^c Roman numerals indicate compounds whose chemical structures are unknown.
^d A = 9-hydroxy dieldrin.
^e B = 9-keto dieldrin.

Table 38.—R_t values and amounts, in parts per million, of dieldrin^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0074	15.16	2.03	0.536	5.14	2.82	232.3	1.35	12.57
I ^c	0.65	...	...	...	...	...	0.23	0.866	...	...
Dieldrin	0.58	0.0020	14.96	2.03	0.495	5.07	2.56	229.87	...	12.29
II	0.43	...	...	...	...	...	...	0.456	...	...
A ^d	0.38	0.20	...	...	...	...	...	1.11	...	0.19
B ^e	0.31	...	...	...	0.043	...	...	...	...	0.07
III	0.18	0.00034	...	...	...	...	...	...	...	...
IV	0.12	0.00025	...	...	...	...	...	...	...	...
V	0.07	0.00035	...	...	...	...	...	...	...	...
VI	0.04	0.00101	...	...	...	...	...	...	...	...
Origin	0.00	0.00157	...	...	...	...	...	...	...	...
Unextractable ¹⁴ C		...	1.23	0.028	0.177	0.10	0.14	1.78	0.25	0.65

^a 1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-*exo*, *endo*-5,8-dimethanonaphthalene, ¹⁴C-ring.^b Silica Gel GF-254, ether-*n*-hexane, 3:2 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = 9-hydroxy dieldrin.^e B = 9-keto dieldrin.

Table 39.—R_f values and amounts, in parts per million, of toxaphene^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.04441	13.2941	17.6198	2.2570	10.3977
Toxaphene	0.70	0.00159	10.9743	15.2637	1.4147	6.7523
I ^c	0.57	0.00106	1.7535	1.8360	0.2359	2.4923
II	0.51	0.00076	...	0.2961	...	0.5022
III	0.45	0.00099	0.3589	0.0863	...	0.3161
IV	0.34	0.00164	0.1130	0.0585	trace	0.1487
V (strip)		0.00429	...	...	0.4042	...
VI	0.03	0.00078	...	...	...	0.0187
Origin	0.00	0.02002	0.0944	0.0211	0.2022	0.1674
Unextractable ¹⁴ C		0.01328	2.2156	1.1153	1.1245	4.2264

^a C₁₀H₁₀Cl₈ (67–69% chlorinated camphene), 8-¹⁴C.^b Silica Gel GF-254, Skellysolve B (b.p. 68°C): diethyl ether:acetone, 80:20:10 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 40.—R_f values and amounts, in parts per million, of endrin^a and its degradation products found in the water and organisms of a model ecosystem^b.

	R _f ^c	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> ^d (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0135	13.62	150.58	...	4.48
I ^e	0.81	...	0.48	5.07	...	...
Endrin	0.73	0.00254	11.56	125.00	...	3.40
II	0.53	0.00385	1.58	6.55	...	1.04
III	0.42	trace	trace	5.87	...	...
IV	0.31	trace	trace	2.69	...	...
Origin	0.00	0.00436	...	1.85	...	0.04
Unextractable ¹⁴ C		0.0027	...	...	...	...

^a 1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-*endo*, *endo*-5,8-dimethano-naphthalene, ¹⁴C-ring.^b Experiment terminated after 63 days.^c Silica Gel GF-254, *n*-hexane:diethyl ether, 1:1 by volume.^d Mosquito larvae killed throughout experiment.^e Roman numerals indicate compounds whose chemical structures are unknown.Table 41.—R_f values and amounts, in parts per million, of lindane^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0232	0.375	3.70	0.75	1.02
A ^c	0.55	...	...	2.50	...	...
Lindane	0.47	0.00167	...	0.762	...	0.935
I ^d	0.27	0.000084	...	...	...	...
II	0.19	0.00304	...	...	...	...
III	0.14	0.00276	...	...	...	...
IV	0.09	0.00636	...	0.248	...	...
Origin	0.00	0.00877	0.375	0.185	...	0.085

^a *gamma*-1,2,3,4,5,6-hexachlorocyclohexane, ¹⁴C-ring.^b Silica Gel GF-254, *n*-hexane:acetone, 9:1 by volume.^c A = *gamma*-pentachlorocyclohexene.^d Roman numerals indicate compounds whose chemical structures are unknown.

Table 42.— R_f values and amounts, in parts per million, of mirex^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.018	9.70	18.40	13.60	3.50
Mirex	0.95	0.0157	9.49	18.29	13.54	3.45
Origin	0.00	0.0023	0.21	0.11	0.06	0.05

^a Dodecachloro-octahydro-1,3,4-metheno-2-H-cyclabuta-[c,d]-pentalene, ¹⁴C-ring.^b Silica Gel GF-254, chloroform.Table 43.— R_f values and amounts, in parts per million, of heptachlor^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.02225	0.8448	2.7515	3.1258	2.0603
Heptachlor	0.64	0.00003	0.6219	1.1146	0.9421	0.1146
Heptachlor epoxide	0.56	0.00021	0.1877	1.0659	1.5332	1.6293
I ^c	0.43	0.00002	...	0.0217	0.0434	...
II	0.37	0.00001	...	0.1142	0.0328	...
III	0.32	0.00005	...	0.0490	0.0244	...
1-hydroxychlorodene	0.21	0.00040	...	0.0597	0.0791	0.0471
1-hydroxychlorodene epoxide	0.14	0.00659	...	0.2066	0.2694	0.1211
IV	0.07	0.00036	...	0.0272	0.0763	0.1010
V	0.03	0.00026	...	0.0055	0.0244	...
Origin	0.00	0.00677	0.0352	0.0871	0.1007	0.0472
Unextractable ¹⁴ C		0.00755	0.4079	0.1646	0.2363	1.5479

^a 1-*exo*-4,5,6,7,8,8-heptachloro-3a,4,7,7a-tetrahydro-4,7-methanoindene, ¹⁴C-ring.^b Silica Gel GF-254, cyclohexane:diethyl ether, 80:20 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 44.— R_f values and amounts, in parts per million, of heptachlor epoxide^a and its degradation products found in the water and organisms of a model ecosystem.

	R_f^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> ^c (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00638	2.2620	101.9105	...	8.8807
Heptachlor epoxide	0.63	0.00125	2.0618	83.0774	...	6.1100
A ^d	0.18	0.00036	0.0800	8.8663	...	1.7114
Origin	0.0	0.00200	0.1202	9.9668	...	1.0595
Unextractable ¹⁴ C		0.00277	1.1602	0.1110	...	0.8554

^a 1-*exo*-4,5,6,7,8,8-heptachloro-*exo*-2,3-epoxy-3a,4,7,7a-tetrahydro-4,7-methanoindane, ¹⁴C-ring.^b Silica Gel GF-254, cyclohexane, diethylether, 80:20 by volume.^c All killed during the experiment.^d A = 1-hydroxychlorodene epoxide.

Table 45.—R_f values and amounts, in parts per million, of chlordane^a and its degradation products found in the water and organisms of a model ecosystem.

	R _f ^b	Water	<i>Oedogonium</i> (alga)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.017718	110.3415	154.189	13.645	11.243
I ^c	0.92	...	0.974	2.199	...	0.451
II	0.90	...	0.664	...	...	...
III	0.84	0.000059	1.905	5.751	3.602	1.405
IV	0.78	...	1.708	...	5.502	...
V	0.73	...	...	...	...	0.658
Chlordane ⁺	0.70	0.00106	104.289	140.570	6.500	8.754
VI	0.64	...	...	1.541	...	...
VII	0.55	0.0000135	...	0.244	...	...
VIII	0.47	0.0000027	...	...	...	...
IX	0.28	0.00127	0.474	2.088	0.509	0.217
X	0.23	0.000176	...	...	...	...
XI	0.19	0.0000939	...	...	...	0.0260
XII	0.17	0.000264	...	...	...	...
XIII	0.15	0.000415	0.358	0.478	0.339	0.0223
XIV	0.12	0.000438	0.180	0.398	...	...
XV	0.10	...	...	0.884	...	0.0744
XVI	0.06	0.000689	...	...	...	...
XVII	0.04	0.000501	...	...	...	...
XVIII	0.03	0.009305	...	...	...	...
XIX	0.02	...	0.325	...	...	...
XX	0.01	...	0.238	...	...	...
Origin	0.00	0.0123	0.324	1.516	2.169	0.205
Unextractable ¹⁴ C		0.00752	100.0847	1.752	6.920	2.450
cis: trans		4.02	3.08	5.39	...	6.98

^a 1,2,4,5,6,7,8,8-octachloro-3a,4,7,7a-tetrahydro-4,7-methanoindane (cis:trans, 3:1), ¹⁴C-ring.^b Silica Gel GF-254, n-hexane:ethyl acetate, 9:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.

Table 46.—R_t values and amounts, in parts per million, of captan^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Daphnia</i> (water flea)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.001789	0.865	0.393	0.301	0.0462	0.0522
I ^c	0.93	...	0.0278	...	0.0592	...	...
II	0.85	...	0.0077	...	0.0795	...	...
III	0.81	...	...	...	0.0679	...	0.0492
IV	0.79	...	0.0166	...	...	...	...
V	0.68	...	...	...	...	...	...
VI	0.39	...	0.0105	...	...	...	...
VII	0.35	0.00000426	...	...	...	...	...
VIII	0.33	...	0.0142	...	...	...	...
IX	0.26	0.0000096	...	...	...	...	...
X	0.25	0.00000893	0.0608	...	...	...	...
XI	0.18	0.00000456	...	...	...	...	...
XII	0.14	0.0000109	...	...	...	...	...
XIII	0.10	0.00000365	0.590	...	...	...	...
XIV	0.053	0.0000891	0.0159	...	...	...	0.00215
Origin	0.00	0.0000353	0.122	...	0.0940	...	0.000861
Unextractable ¹⁴ C		0.001623	0.967	0.338	0.0998	0.0584	0.0158

^a N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide, ¹⁴C-trichloromethyl.^b Silica Gel GF-254, petroleum ether-acetone, 4:1 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.Table 47.—R_t values and amounts, in parts per million, of hexachlorobenzene^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Daphnia</i> (water flea)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.00695	1.827	0.696	4.098	0.737	3.155
Hexachlorobenzene	0.80	0.00298	1.556	0.598	3.72	0.429	0.857
A ^c	0.50	0.00034	...	...	...	...	...
I ^d	0.10	0.00023	...	...	...	...	0.446
II	0.05	...	...	...	...	0.0385	0.857
Origin	0.00	0.000143	0.271	0.098	0.378	0.269	0.995
Unextractable ¹⁴ C		0.00197	...	...	...	...	...

^a 1,2,3,4,5,6-hexachlorobenzene, ¹⁴C-ring UL.^b Silica Gel GF-254, benzene:acetone, 1:1 by volume.^c A = Pentachlorophenol.^d Roman numerals indicate compounds whose chemical structures are unknown.

Table 48.—R_t values and amounts, in parts per million, of pentachlorophenol^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	Sand	<i>Oedogonium</i> (alga)	<i>Daphnia</i> (water flea)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.05235	0.0186	0.8061	6.2441	2.9576	1.3355	4.3765
I ^c	0.86	0.00028	0.0005	0.0673	...	0.0438	...	0.0197
Pentachlorophenol	0.64	0.01693	0.0048	0.0893	3.4692	0.3619	0.4451	2.2408
II	0.56	0.00109	0.0010	0.0771	...	...	...	...
III	0.49	...	...	0.0575	...	...	...	...
IV	0.42	...	...	0.0477	...	0.8122	...	...
V	0.33	0.00009	0.0023	0.0440	...	...	...	...
VI	0.22	0.00010	0.0011	0.1700	...	0.3129	...	...
VII	0.15	0.00008	0.0013	...	...	0.2798	...	...
VIII	0.10	...	0.0020	...	...	...	...	...
IX	0.05	0.00012	...	0.0808	...	...	...	...
Origin	0.00	0.02220	0.0056	0.1724	2.7749	1.1470	0.8904	2.1160
Unextractable ¹⁴ C		0.01146	...	...	...	...	...	...

^a 2,3,4,5,6-pentachlorophenol, ¹⁴C-ring UL.
^b Silica Gel GF-254, n-hexane:acetone:acetic acid, 80:20:2 by volume.
^c Roman numerals indicate compounds whose chemical structures are unknown.

Table 49.—R_t values and amounts, in parts per million, of banamite^a and its degradation products found in the water and organisms of a model ecosystem.

	R _t ^b	Water	<i>Oedogonium</i> (alga)	<i>Corbicula</i> (clam)	<i>Uca</i> (crab)	<i>Daphnia</i> (water flea)	<i>Elodea</i> (aquatic plant)	<i>Physa</i> (snail)	<i>Culex</i> (mosquito)	<i>Gambusia</i> (fish)
Total ¹⁴ C		0.0271	3.194	2.341	1.365	0.941	1.872	17.553	4.153	2.322
Banamite	0.75	0.0000186	...	...	0.0156	...	0.0410	...	0.0736	...
I ^c	0.61	0.0000930	...	...	...	...	0.0928	0.565	0.266	...
II	0.53	0.000539	0.963	2.044	0.0670	0.686	1.048	10.635	0.453	1.624
III	0.35	0.00115	0.181	...	0.0568	...	0.0662	1.160	0.265	0.378
A ^d	0.27	0.000294	0.142	...	0.0364	...	0.0515	0.306	0.300	...
IV	0.21	0.000294	0.202	...	...	...	...	...	...	...
V	0.14	0.000850	0.269	0.227	0.0406	...	0.185	2.5493	0.324	0.0943
VI	0.07	0.00248	...	...	...	...	...	0.938	0.286	0.0452
VII	0.03	0.00428	0.514	...	0.140	...	0.059	0.478	0.533	...
Origin	0.00 /	0.0111	0.923	0.0703	1.009	0.255	0.328	0.872	1.652	0.180
Unextractable ¹⁴ C		0.00599	6.602	0.136	1.088	0.877	1.445	1.777	2.137	0.451

^a Benzoylchloride-2,4,6-trichlorophenylhydrazine, ¹⁴C benzoyl ring.^b Silica Gel GF-254, n-hexane-ethyl acetate, 80:20 by volume.^c Roman numerals indicate compounds whose chemical structures are unknown.^d A = Benzoic acid-2,4,6-trichlorophenyl hydrazide.

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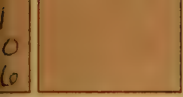
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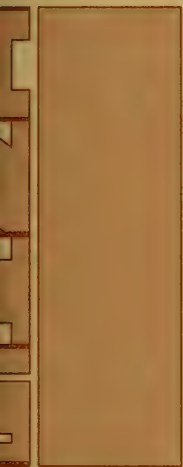
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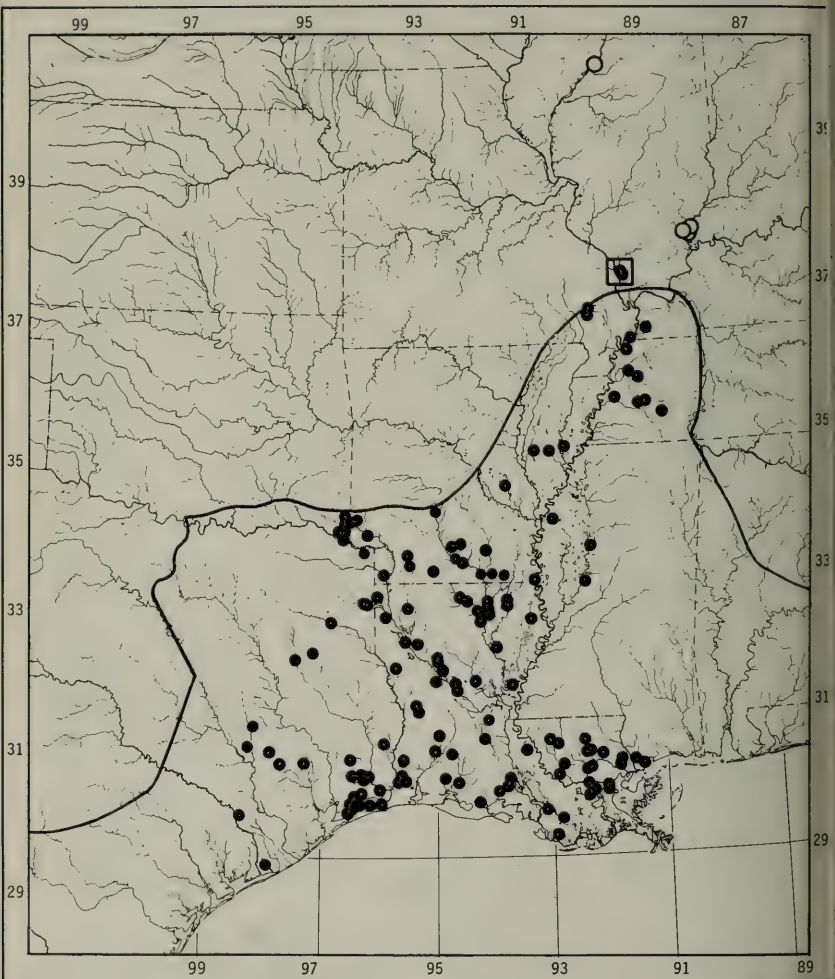


Fig. 1.—Distribution of *Lepomis symmetricus* in relation to the Coastal Boundary (solid black line). Solid circles represent recent localities (1938 to the present); large open circles represent old records (pre-1900) where the species is presumably extinct. The most northern open circle also represents the type-locality. The life-history study area is enclosed within the square.

The Bantam Sunfish, *Lepomis symmetricus*: Systematics and Distribution, and Life History in Wolf Lake, Illinois

Brooks M. Burr

The bantam sunfish, described as *Lepomis symmetricus* by Stephen A. Forbes in 1883, is one of the least known species in the genus, probably because of its small size, rarity over parts of its range, occurrence in rather inaccessible swamp habitats, and drab and nondescript appearance. This effort to remedy the gaps in our knowledge of the species reviews all published references to *L. symmetricus*. To supplement the meager information available, this report includes an analysis of morphological variation based on the study of museum specimens, an assessment of the species' distribution, and a life-history study based on periodic collections made at a study site in southern Illinois.

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Unless stated otherwise, the majority of the specimens used in this study are deposited at the Illinois Natural History Survey (INHS).

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METHODS AND MATERIALS

An attempt was made to compile as complete a synonymy as possible for *Lepomis symmetricus*, and it is believed that virtually all published references to it have been examined. Morphological data were taken on selected series that could be expected to show geographical variation, allometric variation, or sexual dimorphism in the species. Meristic and morphometric data were taken in the conventional manner of Hubbs & Lagler (1964: 19-26). One-way analysis of variance tests were run to determine significant differences in means of samples determined by sex. Unless stated otherwise, measurements are standard lengths (SL).

Observations and minnow-seine collections were made in Wolf Lake in Union County, Illinois, at approximately 1-month intervals, except during the spawning season, when more frequent observations were needed. The life-history study began 2 June 1973 and ended 27 May 1975.

Specimens were preserved in 10-percent formalin and were returned to the laboratory for study. In all, 233 specimens from Wolf Lake were preserved and examined. Because the species is protected by the Illinois Fish Code, usually no more than 20 specimens were taken on one visit even when the species was commonly encountered, so as not to seriously decimate the population. Collecting was done by bag seine; minnow seine; dip net; and, in one instance, by electrofishing. Potential predators of the bantam sunfish were occasionally collected for examination of stomach contents. Field notes were routinely taken. In the laboratory, specimens were sexed, measured, and aged, and their gonads and stomachs were excised and studied. During the spawning season, breeding adults were brought to the laboratory and placed in observation tanks.

Aging to year class was done by counting scale annuli removed from the dorsum. Aging to month was done by using May, the month of greatest breeding activity in Wolf Lake, as month zero. Thus, a sunfish collected in October with one scale annulus was estimated to have lived 1 year and 5 months. For certain comparisons sunfishes were divided into young (through 12 months) and adult (over 12 months) age groups.

Weights of the ovaries of 30 females were obtained and recorded as a proportion of the adjusted body weight (the specimen minus the ovaries, stomach, intestine, and liver) of the female. Mature ova from 14 preserved breeding females were counted. Indicators used for ascertaining probable spawn-

ing periods in other localities and other years were that males exhibited breeding color patterns and that females were heavy with ova.

The relative survival of each year class of the study population was calculated by expressing the number of individuals in that year class as a proportion of the number of individuals in a younger year class.

SYSTEMATICS

SYNONYMY

Lepomis symmetricus Forbes

Lepomis symmetricus McKay 1882: 88 (*nomen nudum*); Forbes in Jordan & Gilbert 1883: 473-474 (original description, Illinois River [at Pekin] Illinois); Forbes 1884: 68 (Illinois range); Jordan 1884: 320-321 (redescription, museum specimens cited); Jordan 1888: 117 (redescription); Bollman 1892: 566, 571 (key, range); Evermann & Kendall 1894: 84, 93, 111 (redescription, Texas records); Hay 1894: 255, 261 (redescription, key, not taken in Indiana); Richardson 1904: 31, 33 (relationships, key, Illinois range); Forbes & Richardson 1908: 251-252 (redescription, key, Illinois range); Forbes 1909: 388 (Illinois range); Pratt 1923: 118 (key, range); Greene 1927: 309 (not in Wisconsin); Hildebrand & Towers 1927: 133-134 (Greenwood, Mississippi, food habits in Mississippi); Summers 1937: 434 (new trematode parasite, Baton Rouge, Louisiana); Mizelle 1938: 160 (trematode transferred to new genus); Mizelle & Hughes 1938: 351 (trematode parasite cited); Summers & Bennett 1938: 248 (trematode parasite cited); Kuhne 1939: 110 (Tennessee list, redescription, sexes figured); Lamb 1941: 45 (Willow Creek, San Jacinto drainage, Texas); Fowler 1945: 364, 370 (Louisiana and Mississippi records, figure erroneous); Gerking 1945: 115 (possible

in Indiana); Seamster 1948: 165, 168 (trematode parasite cited); Baughman 1950: 247 (Texas list); Moore & Cross 1950: 146 (recorded from Oklahoma); Reeves & Moore 1951: 42 (Oklahoma Coastal Plain); Böhlke 1953: 71 (SU syntypes listed); Moore 1952: n.p. (Oklahoma list); Jurgens & Hubbs 1953: 15 (Texas list); Knapp 1953: 115 (key, Texas range); Gunning & Lewis 1955: 556 (habitat, food habits in Illinois); Gunning & Lewis 1956: 24 (Wolf Lake and Pine Hills, Illinois); Eddy 1957: 191 (key, range); Hubbs 1957a: 97 (Texas range); Hubbs 1957b: 9 (Texas list); Moore in Blair *et al.* 1957: 170 (key, range); Hubbs 1958: 10 (Texas list); Boudreaux *et al.* 1959: 8, 10 (Sour Lake, Hardin County, Texas); Cook 1959: 180 (redescription, ecology, Mississippi range); Bailey *et al.* 1960: 27 (list); Smith & Bridges 1960: 254 (INHS syntypes); Hubbs 1961: 10 (Texas range); Branson & Moore 1962: 9, 15, 24, 27, 29, 31, 33, 41, 48, 65, 72, 91, 99 (relationships, acoustico-lateralis system); Clay 1962: 119 (Kentucky range); Collette 1962: 146, 177 (associate of slough darter and swamp darter); Lambou 1962: 78 (Lake Bistineau, Louisiana); Walker 1962: 40 (Jackson, Lincoln, and Bienville parishes, Louisiana); Walker 1963: 48 (Choudrant Bayou, Louisiana); Sharma 1964: 533 (mucus cells in canal linings); Burton & Douglas 1965: 94 (Bayou De Siard, Louisiana); Smith 1965: 9 (Illinois range); Pflieger 1966: 53 (Missouri key); Breder & Rosen 1966: 413 (breeding habits unknown); Childers 1967: 160 (tribe Lepomini); Douglas & Davis 1967: 23 (Louisiana list); Hoffman 1967: 340 (known parasites); Pflieger 1968: 54 (Missouri key); Moore in Blair *et al.* 1968: 128-129 (key, range); Whitaker 1968: 96-97 (key, range); Eddy 1969: 217 (key, range);

Smith & Sisk 1969: 66 (Obion Creek, Kentucky); Bailey *et al.* 1970: 36 (list); Jenkins *et al.* 1971: 74 (possibly present in lower Tennessee or Cumberland rivers); Pflieger 1971: 413-414 (habitat, zoogeography, Missouri range); Smith *et al.* 1971: 10 (not in upper Mississippi River); Hubbs 1972: 6 (Texas range); Miller 1972: 244 (threatened in Illinois and Missouri); Rozenburg *et al.* 1972: iii, 22, 28, 30, 32, 33, 36, 40, 45, 51, 82, 111 (Navasota River, Texas); Buchanan 1973a: 29 (Arkansas list); Buchanan 1973b: 51 (key, Arkansas range); Miller & Robison 1973: 184-185 (key, redescription, ecology, Oklahoma range); Moore 1973: 6 (McCurtain County, Oklahoma); Smith 1973: 33 (Illinois key); Lopinot & Smith 1973: 46-47 (status in Illinois); Buchanan 1974: 89 (status undetermined in Arkansas); Douglas 1974: 312-313 (redescription, Louisiana range); Pflieger in Holt *et al.* 1974: n.p. (rare in Missouri); Ackerman 1975: 10 (endangered in Illinois); Boyd *et al.* 1975: 11, 21 (status in Illinois); Clay 1975: 267, 276, 280 (redescription, key, Kentucky range); Douglas & Davis 1975: 23 (Louisiana list); McReynolds 1975: 253 (LaRue Swamp, Illinois); Pflieger 1975: 254, 265 (figure, key, redescription, Missouri range); Robison 1975: 54, 56 (Saline River, Arkansas, evidence of recent

spawning); Webb & Sisk 1975: 63, 67, 69 (Bayou de Chien, Kentucky, endangered in Kentucky); Hubbs 1976: 6 (Texas list); Hubbs & Pigg 1976: 116 (indeterminate status in Oklahoma); Seehorn 1976: 21 (South-eastern National Forest list).

Apomotis symmetricus: Boulenger 1895: 21 (redescription); Jordan & Evermann 1896: 998-999 (redescription); Evermann 1899: 310 (Lake Lapourde, Louisiana); Large 1903: 24 (Illinois range); Jordan *et al.* 1930: 299 (list, range); Gowanloch 1933: 348, 351 (Louisiana range); Schlaikjer 1937: 12 (phylogeny); Schrenkeisen 1938: 243-244 (redescription, range).

Lethogrammus symmetricus: Hubbs in Jordan 1929: 147 (transfer to new genus erected by C. L. Hubbs); Greene 1935: 220 (not in Wisconsin); O'Donnell 1935: 486 (Illinois range); Breder 1936: 28 (breeding habits unknown); Baker 1937: 48 (redescription, rare at Reelfoot Lake); Baker & Parker 1938: 162 (Reelfoot Lake list); Baker 1939a: 34 (redescription, sexes figured, common at Reelfoot Lake); Baker 1939b: 45 (Reelfoot Lake key).

TYPES

Lepomis symmetricus was described by Forbes in Jordan & Gilbert (1883: 473-474) from a syntypic series consisting of 15 specimens collected 16 April

Table 1.—Frequency distribution for number of caudal peduncle scales in selected populations of *Lepomis symmetricus*.

Drainage	Number of Scales						N	Mean	Standard Deviation	Coefficient of Variation
	17	18	19	20	21	22				
Illinois R., Ill.	..	..	6	4	1	..	11	19.5	0.69	3.5
Wabash R., Ill.	..	..	..	3	7	2	12	20.9	0.67	3.2
Mississippi R., Ill., Mo., Ky.	..	3	13	13	17	5	51	20.2	1.21	6.0
Mississippi R., Tenn.	..	..	12	13	..	..	25	19.5	0.51	2.6
Mississippi R., Ark., La.	1	3	10	9	2	..	25	19.3	0.95	4.9
Ouachita R., Ark., La.	4	5	11	4	2	..	26	18.8	1.13	6.0
Red R., Okla., Tex., Ark., La.	5	12	10	5	1	..	33	18.5	1.03	5.6
Gulf Slope, Tex., La.	7	7	10	9	6	..	39	19.0	1.34	7.1

Table 2.—Frequency distribution for number of lateral line scales in selected populations of *Lepomis symmetricus*.

Drainage	Number of Scales										N	Mean	Standard Deviation	Coefficient of Variation
	30	31	32	33	34	35	36	37	38					
Illinois R., Ill.	..	..	7	2	2	..	..	..	..	11	32.5	0.82	2.5	
Wabash R., Ill.	..	..	..	..	3	5	1	2	1	12	35.4	1.51	4.3	
Mississippi R., Ill., Mo., Ky.	..	2	12	15	9	5	3	4	1	51	33.6	2.87	8.5	
Mississippi R., Tenn.	..	2	4	6	7	4	2	..	..	25	33.5	1.39	4.2	
Mississippi R., Ark., La.	1	1	5	7	4	4	3	..	..	25	33.4	1.58	4.7	
Ouachita R., Ark., La.	2	3	5	4	4	4	3	1	..	26	33.3	1.95	5.9	
Red R., Okla., Tex., Ark., La.	6	4	10	7	6	..	..	..	..	33	32.0	1.39	4.3	
Gulf Slope, Tex., La.	5	4	10	8	8	3	1	..	..	39	32.6	1.57	4.8	

Table 3.—Frequency distribution for number of dorsal soft rays in selected populations of *Lepomis symmetricus*.

Drainage	Number of Rays				N	Mean	Standard Deviation	Coefficient of Variation
	9	10	11	12				
Illinois R., Ill.	..	7	3	1	11	10.5	0.69	6.6
Wabash R., Ill.	2	9	1	..	12	9.9	0.51	5.2
Mississippi R., Ill., Mo., Ky.	..	23	24	4	51	10.6	0.40	3.8
Mississippi R., Tenn.	..	17	6	2	25	10.4	0.65	6.3
Mississippi R., Ark., La.	3	18	4	..	25	10.0	0.54	5.4
Ouachita R., Ark., La.	3	19	3	1	26	10.1	0.63	6.2
Red R., Okla., Tex., Ark., La.	4	17	12	..	33	10.2	0.66	6.5
Gulf Slope, Tex., La.	4	22	10	3	39	10.3	0.77	7.5

Table 4.—Frequency distribution for number of anal soft rays in selected populations of *Lepomis symmetricus*.

Drainage	Number of Rays				N	Mean	Standard Deviation	Coefficient of Variation
	9	10	11	12				
Illinois R., Ill.	..	10	..	1	11	10.2	0.60	5.9
Wabash R., Ill.	1	9	2	..	12	10.1	0.51	5.0
Mississippi R., Ill., Mo., Ky.	11	22	17	1	51	10.2	0.61	6.0
Mississippi R., Tenn.	7	17	1	..	25	9.8	0.52	5.3
Mississippi R., Ark., La.	8	15	2	..	25	9.8	0.60	6.1
Ouachita R., Ark., La.	8	17	1	..	26	9.7	0.53	5.5
Red R., Okla., Tex., Ark., La.	3	21	9	..	33	10.2	0.58	5.7
Gulf Slope, Tex., La.	9	27	3	..	39	9.8	0.54	5.5

and 2 June 1880 from the Illinois River (Mississippi drainage) at Pekin, Tazewell County, Illinois (Fig. 1). All 15 of the original syntypes are extant: INHS 220 (8, 32.7–39.5 mm SL); INHS 226 (2, 50.1–51.2 mm SL); MCZ 25014 (1, 49.5 mm SL); SU 1276 (3, 49.8–56.9 mm SL); USNM 29864 (1, 51.0 mm SL). All 15 are in a good state of preservation. To preserve customary nomenclature and in accordance with the International Code of Zoological Nomenclature Article 74, recommendation 74D, a lectotype of *L. symmetricus* Forbes is herewith designated (INHS 75004, 39.5 mm SL). The specimen, a juvenile, conforms to the characterization of the species given under Description and in Tables 1–4. The incomplete lateral line has 34 scales with 6 scales above and 13 scales below the lateral line. There are 19 caudal peduncle scales, 5 cheek row scales, and 6 branchiostegal rays. Fin ray counts are: dorsal spines, 10; anal spines, 3; pectoral rays, 12–12; dorsal soft rays, 10; anal soft rays, 10. The nine other specimens originally accessioned as

INHS 220 and 226 are paralectotypes, now INHS 75005 and INHS 75006, respectively. The USNM, SU, and MCZ syntypes also became paralectotypes, keeping their original catalogue numbers.

It is unlikely that the original material of *L. symmetricus* collected by Forbes and associates was captured from the Illinois River proper. Although the Illinois River has changed rather drastically since Forbes's era, it probably never maintained habitat suitable for *L. symmetricus*. More likely the specimens came from one of the natural floodplain lakes in the Pekin area, where favorable habitat has been present in past years.

DIAGNOSIS

The most diminutive species of *Lepomis* (the largest specimen measured is 75.5 mm SL) is distinguished from other members of the genus by this combination of characters: Lateral line incomplete (1–18 scales unpored) or interrupted (as many as 6 times). Gill rakers long (longest in the genus,

Table 5.—Proportional measurements of *Lepomis symmetricus* from throughout the range, expressed in thousandths of standard length.*

Measurement	10 Males (54–64 mm SL)				10 Females (50–64 mm SL)			
	Range	Mean	Standard Deviation	Coefficient of Variation	Range	Mean	Standard Deviation	Coefficient of Variation
Head length	375–423	396	013	3.5	361–403	390	012	3.2
Body depth	471–531	491	018	3.6	468–527	494	017	3.4
Caudal-peduncle depth	150–169	160	006	3.6	142–192	163	014	8.8
Pectoral fin length	245–285	263	014	5.4	248–291	263	012	4.7
Pelvic fin length	227–255	238	009	3.9	212–243	225	010	4.6
Longest dorsal spine	116–153	139	010	7.2	126–164	140	014	9.7
Head width	180–219	203	013	6.5	191–234	213	013	6.0
Bony interorbital width	078–096	087	006	6.6	074–093	084	007	7.8
Snout length	071–086	078	005	6.7	074–088	081	006	7.4
Upper jaw length	123–151	140	009	6.2	124–158	133	010	7.8
Predorsal length	439–480	459	014	3.0	445–483	462	014	2.9
Base dorsal fin length	461–508	478	015	3.1	455–517	480	017	3.6
Longest anal spine	120–151	137	010	6.9	124–157	139	012	8.7
Base anal fin length	216–297	244	022	8.8	206–257	234	015	6.6
Orbit length	087–105	095	005	5.7	083–105	095	002	7.8

* Based on NLU 29918, 12804, 1954; UT 90.116, 90.140; TCWC 3643; HWR 74–8; INHS 75020, 75021, 75022, 75023, 18151, 18143, 17547.

longest rakers 2.3–2.9 mm), and slender (0.3–0.5 mm wide, 7–9 times longer than wide), numbering 12–15, modally 13. Opercle stiff to its bony margin, the dark opercular spot slightly diffuse on narrow, bordering membrane. Dorsal coloration dusky with dark coffee-colored spots on body, spots occasionally forming irregular vertical bands. Head and cheeks darkened and without patterns. Juveniles often more vertically barred than adults and have a prominent black blotch in the posterior rays of the soft dorsal fin, becoming less intense with age. Branson & Moore (1962) showed these additional characters to be distinctive: only one posterior pore on the post-temporal, lateralis ending under the soft dorsal fin, preopercle angle 110° to 115° , lachrymal bone nearly twice as tall as wide, supramaxilla shorter than maxilla, and no teeth on tongue or pterygoids.

DESCRIPTION

Forbes (*in* Jordan & Gilbert 1883:

473–474) and Forbes & Richardson (1908: 251–252) adequately described the specimens available to them. The following description is an amplification, which includes additional meristic and morphometric data, and a more comprehensive description of coloration. Body proportion values are presented in Table 5. When no geographic variation was noted, the variation data from throughout the range of the species are merely summarized. When geographic variation was noted, the ranges and modes are given in the description, but their frequencies are discussed under Variation. Counts of lateral-line scales, caudal-peduncle scales, dorsal soft rays, and anal soft rays, all of which show slight clinal variation, are presented in Tables 1–4. General physiognomy and pigmentation of adults and juveniles are shown in Fig. 2 and 3.

Lateral line scales 30–38, modally 32 (Table 2). Bailey (1938) reported one specimen with 40 lateral line scales. Scales above the lateral line 5 (in 7

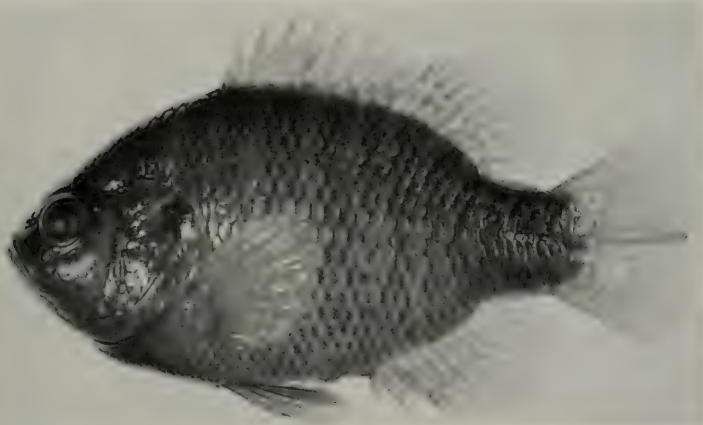


Fig. 2—Breeding male *Lepomis symmetricus* 53.6 mm in standard length collected in Wolf Lake on 27 May 1975. Pigmentation in the fins is somewhat subdued by preservation.

specimens), 6 (92), 7 (11), $\bar{x} = 6.1$. Scales below the lateral line 12 (in 48 specimens), 13 (52), 14 (15), $\bar{x} = 12.7$. Caudal peduncle scales 17–22, modally 19 (Table 1). Scales on cheek 4–6, modally 5. Scales well developed on preopercle, subopercle, interopercle, and opercle, all such scales about the same size and shape. No scales on top of head.

Dorsal spines 9 (in 22 specimens), 10 (133), 11 (6), $\bar{x} = 9.9$. Dorsal soft rays 9–12, modally 10 (Table 3). Anal spines 2 (in 1 specimen), 4 (2), 3 in all others. Anal soft rays 9–12, modally 10 (Table 4). Pectoral rays 11 (in 8 specimens), 12 (66), 13 (32), $\bar{x} = 12.2$. All pelvic fins counted had 1 spine. Pelvic rays 4–4 (in 1 specimen), 4–5 (2), 5–5 (42). Principal caudal rays 17 (in 41 specimens), 18 (1).

Gill rakers on first arch (all rudiments counted) 12 (in 12 specimens), 13 (36), 14 (22), 15 (6), $\bar{x} = 13.3$. Rakers long and slender (see Diagnosis). Rudimentary rakers (usually 3–5) are shorter and more blunt. The lateral line on the body is incomplete or interrupted (see Diagnosis and Fig. 3). The cephalic lateral-line system was described in detail by Branson & Moore (1962). Caudal fin slightly emarginate. No teeth on tongue and pterygoids. Teeth present on vomers and palatines. Pharyngeal arches narrow with many small, blunt subconical teeth present (Richardson 1904). Peritoneal color is usually fleshy with many scattered melanophores, but occasional specimens have a more silvery ground color with melanophores scattered throughout.

Dorsal coloration is dusky olive-brown or, in life, dark green with a somewhat lighter venter of yellowish brown. Many dark coffee-colored spots occur over the body, often one spot per scale, creating vague, irregular vertical bands or longitudinal rows. The belly, breast, throat, and chin have many tiny, dark melanophores. Some spec-

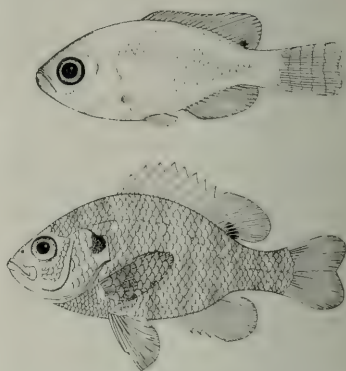


Fig. 3.—*Lepomis symmetricus* prejuvenile 12.0 mm in standard length (above) and juvenile 30.0 mm in standard length (below).

imens are almost solid black on the midbody with discrete black punctate marks on the cheeks. The fins, except the pectorals, are dusky overall with the soft dorsal and anal usually having several light spots. The pectoral fin rays are outlined by melanophores but are otherwise clear. The cheeks and head are very dark and have no patterns. The dark opercular spot is usually bordered with a light area on its posterior margin.

Juveniles contrast with adults in generally having more distinct vertical bands, in always having a black spot in the soft dorsal, and in having some red-orange pigmentation in both the soft dorsal and soft anal fins. Juveniles are lighter overall than adults and generally have seven to nine rather distinct vertical bands that are darker (brown) than the overall light greenish ground color. The vertical barring is occasionally obscured by flecks of darker pigment over the body, giving it a spotted appearance. The juveniles of both sexes have a distinct black blotch on the last five to eight rays of the soft

dorsal fin; the pigment is distributed both on the radial and interradial membranes. Rarely, there is a black spot in the soft anal fin (NLU 2907, 2 of 21 specimens; INHS 18151, 1 of 45 specimens) on the last three rays, and again the pigment is both on the radial and interradial membranes. Red-orange pigmentation is also present in the soft dorsal and soft anal fins of both sexes, on the radial and interradial membranes, and is very prominent in specimens collected during the fall and winter months. The belly, breast, throat, and chin sometimes are marked with discrete, tiny brown melanophores. Jordan (1884:320-321) remarked that small specimens from New Orleans had faint blue spots on the sides of their heads. Breeding coloration is discussed under Reproductive Cycles of both sexes.

VARIATION

Sexual

No sexual variation in meristic characters was noted, but some dimorphism in one proportional character and in

sex organs was evident. Pelvic fin length is significantly greater at the 0.05 level ($F = 8.29$) in the male than in the female (Table 5). The urogenital papilla of the adult female is enlarged and protruding during the spawning season, whereas that of the adult male is only slightly enlarged (Fig. 4). The male is not appreciably larger than the female. The largest individuals from the study area were females (61 and 63 mm SL), the largest specimen examined from throughout the range was a female (75.5 mm SL). The largest male was 73.5 mm SL.

Allometric

No allometric variation in meristic characters was found. Although allometric variation in morphometric characters was not investigated, adults are more robust than juveniles, as in other sunfishes. Moreover, it is the adult that is symmetrical in shape and thus is responsible for the trivial name of the species. Juveniles have body proportions similar to those of other juvenile sunfishes. The number of vertical bands, if present at all, is the same in the juvenile and adult. The most notable allometric variation is the tendency for the black spot in the soft dorsal fin to become more diffuse and weak with age. It is prominent in the smallest young and absent in the adult, except in an occasional female. The soft anal and soft dorsal fins have a red-orange coloration that disappears when the fish becomes adult.

Geographic

Geographic variation in some meristic characters was evident when samples were grouped according to major river systems and arranged in a north-to-south order from the Mississippi drainage of Illinois; through the Ouachita and Red river drainages of Arkansas, Oklahoma, Louisiana, and Texas; to

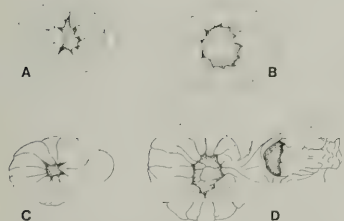


Fig. 4—Genital papillae of *Lepomis symmetricus*. A, nonbreeding male; B, breeding male; C, nonbreeding female; D, breeding female. The nonbreeding specimens were 1+ years old, collected on 19 October 1973; the breeding specimens were 2 years old, collected on 27 April 1974.

the Gulf Coast drainages of Texas and Louisiana (Tables 1-4).

No significant geographic variation was found in any of the body proportions measured (Table 5). In fact, in this respect *L. symmetricus* is remarkably conservative for a species with a rather long north-to-south distribution (Fig. 1). These meristic characters varied clinally: numbers of caudal-peduncle scales, lateral-line scales, and anal soft rays. The number of dorsal soft rays showed a slight but somewhat irregular trend toward more ray elements in the north (Table 3). The Mississippi drainage samples from Arkansas, Louisiana, Tennessee, Missouri, Illinois, and Kentucky were intermediate in caudal-peduncle and lateral-line scale counts between Red River-Gulf Coast samples and those from the Wabash drainage of Illinois. In these counts (Tables 1 and 2) the samples showed a gradual increase toward the north, whereas the soft-ray counts (Tables 3 and 4) were more discordant, with specimens from the Red River-Gulf Coast samples having means close to that of the Illinois River specimens.

The most aberrant samples are those that formerly occurred in oxbow ponds along the Wabash River in White County, Illinois. They have a slightly higher mean number of lateral-line scales and slightly higher mean number of caudal-peduncle scales, but they have lower means for the soft fin ray counts than samples from the upper Mississippi drainage (Tables 1-4).

No apparent geographic trends in coloration or pattern could be perceived. Individual variation occurs in the prominence of the vertical bars and overall darkness, due perhaps in part to the strength of the preservative and age of the individuals.

RELATIONSHIPS

Because of various features of morphology, cytology, and paleontology, *L. symmetricus* has been considered to

be most closely related to *L. cyanellus* (Bailey 1938; Branson & Moore 1962) as a highly specialized congener with several unique characters. Hubbs (in Jordan 1929) considered *L. symmetricus* distinctive enough to warrant placement in a new monotypic genus, *Lethogrammus*, and Bailey (1938), adopting the use of subgenera, placed *L. symmetricus* in the subgenus *Lethogrammus*.

More recent studies on species of *Lepomis* using the techniques of electrophoresis (Avisé & Smith 1974), hybridization (Hester 1970), and chromosome analysis (Roberts 1964) have not included specimens of *L. symmetricus*. Thus, it is not known where the species would be placed in the classification schemes presented by these authors.

SPECIMENS STUDIED

The following list includes only those collections of *L. symmetricus* that were used for meristic and morphometric features. Others were used for the assessment of distribution, descriptive features, and life-history data. Collections are listed generally from north to south. The number of specimens examined is given in parentheses following the catalog number. Specific locality data may be obtained upon request from the author.

Ohio River Drainage

WABASH RIVER SYSTEM.—ILLINOIS, White County: 2 October 1882, INHS 75008 (1); 1 October 1882, INHS 75009 (1); 3 October 1882, INHS 75007 (10).

Mississippi River Drainage

ILLINOIS RIVER SYSTEM.—ILLINOIS, Tazewell County: 16 April 1880, INHS 75004 (1), INHS 75005 (7), USNM 29864 (1); 2 June 1880, INHS 75006 (2).

CLEAR CREEK SYSTEM.—ILLINOIS,

Union County: 18 July 1883, INHS 75102 (5); 16 September 1959, INHS 17547 (6); 27 April 1963, INHS 17566 (1); 27 May 1965, INHS 17583 (1); 31 August 1970, INHS-17557 (1); 21 June 1973, INHS 18143 (5); 25 July 1973, INHS 18151 (2); 24 January 1974, INHS 75025 (6); 28 March 1974, INHS 75022 (1); 30 May 1974, INHS 75021 (1); 27 May 1975, INHS 75020 (1).

OBIION CREEK SYSTEM.—KEN-TUCKY, Hickman County: 21 January 1964, INHS 75024 (1); no date, UL 5617 (10). Fulton County: 15 June 1948, UL 10691 (4).

SAINT FRANCIS RIVER SYSTEM.—MIS-SOURI, Stoddard County: 25 October 1973, INHS 75023 (10).

NATURAL LAKES AND BACKWATERS.—TENNESSEE, Lake County: 11–13 March 1968, UT 90.27 (8); 8 April 1950, FMNH 80532 (2). Lauderdale County: 9 October 1972, UT 90.102 (2). ARKANSAS, Chicot County: 17 August 1974, HWR 74-35 (8).

FORKED DEER RIVER SYSTEM.—TEN-NESSSEE, Haywood County: 3 November 1973, UT 90.138 (1); 27 April 1974, UT 90.140 (6). Gibson County: 19 October 1973, UT 90.139 (10).

L'ANGVILLE RIVER SYSTEM.—AR-KANSAS, St. Francis County: 7 August 1939, UMMZ 128537 (2).

ARKANSAS RIVER SYSTEM.—ARKAN-SAS, Arkansas County: 13 August 1974, ARP-79 (10).

Ouachita River System.—ARKAN-SAS, Bradley County: 23 May 1974, UT 90.116 (1), HWR 74-8 (1); 10 August 1974, HWR 74-26 (7). Calhoun County: 6 October 1974, JLS 74-14 (2). Union County: 25 April 1975, NLU 31455 (10). LOUISIANA, Ouachita Parish: 17 October 1964, NLU 894 (5).

RED RIVER SYSTEM.—ARKANSAS, Little River County: 13 September 1940, UMMZ 170879 (1). OKLA-HOMA, McCurtain County: 20 August 1948, UMMZ 155830 (1). LOU-

ISIANA, Red River Parish: 22 June 1965, NLU 1954 (7). Winn Parish: 23 June 1965, NLU 1989 (7). Caddo Parish: 22 February 1969, NLU 12804 (5). TEXAS, Bowie County: 24 May 1957, TNHC 4984 (10). Harrison County: 17 March 1972, TCWC 4068.14 (2).

LAKE PONTCHARTRAIN.—LOUISI-ANA, Orleans Parish: 15 April 1974, NLU 29918 (5).

Gulf Coast Drainage

CALCASIEU RIVER SYSTEM.—LOUISI-ANA, Calcasieu Parish: 10 August 1965, NLU 2534 (6). Allen Parish: 10 August 1965, NLU 2907 (5). Jefferson Davis Parish: 10 August 1965, NLU 2909 (4).

MERMENTAU-TECHE RIVER SYSTEM.—LOUISIANA, Avoyelles Parish: 20 April 1975, NLU 31572 (3).

NECHES RIVER SYSTEM.—TEXAS, Jefferson County: 2 May 1970, TCWC 3643 (14). Hardin County: August 1950, TNHC 585 (1). Newton County: 7 June 1952, TNHC 2889 (3).

TRINITY RIVER SYSTEM.—TEXAS, Chambers County: 14 July 1953, TNHC 3873 (2).

SAN JACINTO RIVER SYSTEM.—TEXAS, Montgomery County: 23 March 1951, TNHC 1211 (1).

DISTRIBUTION

All known locality records for *L. symmetricus* are plotted in Fig. 1. Along the Gulf Coast the species extends from Eagle Lake (Colorado River drainage, UMMZ 129793) in Texas east to marshes of the Jordan River system in Mississippi. In the Mississippi Valley it presently extends north to the bottomland oxbow lakes and swamps of southern Illinois. A published record for the St. Joseph River of Michigan (Dolley 1933) is clearly based on a misidentification, as Michigan is far out of the range of the bantam sunfish.

L. symmetricus is now almost en-

tirely restricted to the Coastal Plain. It formerly traversed the Coastal Plain boundary far northward to the Illinois River (at Pekin) and backwater ponds and sloughs of the Wabash River system in White County, Illinois (Fig. 1). The species has not been collected from the type-locality since 1880, a fact which Richardson (1904) noted only 24 years after its original description. Indeed, it was collected only twice from Pekin. It has not been collected from the Wabash valley since 1882, whence it was known from three localities and 12 specimens (INHS 75007, 75008, 75009). The distribution of *L. symmetricus* has thus changed rather dramatically in Illinois, the decimation probably being the result of radical changes brought on by human modifications, notably the stocking of non-native sunfishes, a reduction in aquatic vegetation, draining of lowland swamps and sloughs, and various forms of agricultural and industrial pollution (Smith 1971). Mills *et al.* (1966) clearly demonstrated the effects of human modification on the fauna and flora of the Illinois River, and the factors listed above almost surely caused the extirpation of the species from the Pekin area. It is also possible that the relatively short life span of the species (3+ years) is somehow associated with its fairly rapid extirpation from disturbed or polluted areas in the Mississippi Valley of Illinois, Missouri, and Kentucky.

The species is virtually absent east of the Mississippi River in Mississippi. Perhaps the Mississippi River has been an effective barrier to dispersal in this region, or the species' apparent absence there may be because collectors tend to avoid swamps, sloughs, and lowland streams. The species is statewide in occurrence in Louisiana, where it is common, and it is rather common in eastern Texas, southern Arkansas, and parts of western Tennessee (Fig. 1).

The distribution of *L. symmetricus* suggests that it is autochthonous to the lower Mississippi River valley (Pflieger 1971:413-414). It apparently dispersed through oxbow lakes, swamps, and sloughs, created by varying water levels during the history of the Mississippi River. (Pflieger (1971:414) suggested that *L. symmetricus* may have had its origin in the lower Mississippi valley, dispersed northward to central Illinois during the postglacial Climatic Optimum, and become disjunct in its northern distribution subsequently.

CONSERVATION STATUS

Miller (1972) listed *L. symmetricus* as rare in both Illinois and Missouri in a compilation of threatened fishes of the United States. At that time it was known in those states from only two localities: the LaRue-Pine Hills area of southwestern Illinois (Union County) and the Duck Creek Wildlife Area of southeastern Missouri (Bollinger County), where it has been reported to be common (Pflieger 1971:413). It has since been found to be common in Wolf Lake, Illinois, and Mingo National Wildlife Refuge, Missouri (Pflieger 1975:265). The species is on the protected list of both states but not presently endangered in either because its habitat is now rigidly protected in refuges. Recently, Webb & Sisk (1975: 69) recommended that *L. symmetricus* be placed on Kentucky's rare and endangered species list in view of its rarity in Kentucky.

In Oklahoma the species is found only in the swamps of McCurtain County in the southeastern corner of the state (Fig. 1). *L. symmetricus* was not considered threatened by Robison *et al.* (1974) in their list of threatened Oklahoma fishes, but it may presently be reduced in numbers according to Hubbs & Pigg (1976:116). In Arkansas the status of the species was listed as indeterminate by Buchanan (1974).

but *L. symmetricus* was not cited by Robison (1974) in his list of threatened Arkansas fishes. The species is apparently in no danger in southern Arkansas (Fig. 1), where it is known from many localities.

LIFE HISTORY IN WOLF LAKE STUDY AREA

Wolf Lake is a long (ca. 1.9 km), narrow (ca. 0.1 km), and ancient oxbow of the Big Muddy River (Mississippi drainage) situated south of the LaRue-Pine Hills Ecological Area to which it is connected by bottomland swamp. The lake is apparently still in a fairly natural, undisturbed condition and is estimated to be at least 2,000 years old (E. Donald McKay III, personal communication). The northern portion of the lake was recently acquired by the U. S. Forest Service, whereas the southern portion of the lake is privately owned by the Trojan

Powder Plant. Most observations and collections in Wolf Lake were made near the powder plant bridge, where access to the lake was easy although other portions of the lake were sampled.

HABITAT

Wolf Lake is characterized by two predominant habitats: a heavily vegetated shoreline with many submerged logs and stumps (Fig. 5) and an open deepwater area in the center of the lake free from vegetation and submerged objects. The lake is not shaded and the water is usually turbid. The vegetated shoreline, where *L. symmetricus* occurs (Fig. 5), is dominated by spatterdock (*Nymphaea advena*), American lotus (*Nelumbo lutea*), common arrowhead (*Sagittaria latifolia*), coontail (*Ceratophyllum demersum*) and duckweed (*Lemna* spp., *Wolffia* spp.). The bottom consists mostly of decomposed veg-



Fig. 5—Vegetated margin of Wolf Lake, Union County, Illinois, illustrating the preferred habitat of *Lepomis symmetricus*. Photo taken in May 1974.

etation, silt, and mud, with some sand. Water depth ranges from 300 mm to 18 meters. Dissolved oxygen averages 9.0 ppm; temperatures range from 4° to 8° C from December to February and are as high as 29° C in July and August.

L. symmetricus was found in similar habitat during a 1-year study of fishes in the adjacent LaRue-Pine Hills swamp (Boyd *et al.* 1975). During the fall and winter months *L. symmetricus* was characteristically found at a depth of 150–300 mm usually near the shoreline in Wolf Lake. During the summer months the species could be found at depths of 600–1200 mm but still within the vegetated periphery of the lake.

Elsewhere in its range *L. symmetricus* is invariably found in lentic waters characterized by standing timber, submerged logs and stumps, and rich vegetation. Sloughs, oxbows, ponds, backwaters, lakes, and swamps typical of the undisturbed portions of the Coastal Plain are optimal habitat. *L. symmetricus* is found in greatest numbers over substrates consisting of mud, detritus, and decayed plant material.

Although *L. symmetricus* is syntopic with several other species of *Lepomis* in Wolf Lake, it was almost always collected by itself in the areas mentioned. The other *Lepomis* were usually taken in more open areas and generally in deeper water. In Wolf Lake the fishes most often found with *L. symmetricus* in descending order of association were *L. macrochirus*, *L. gulosus*, *Pomoxis nigromaculatus*, *Notemigonus crysoleucas*, *Gambusia affinis*, *Micropterus salmoides*, *Elassoma zonatum*, and *Etheostoma gracile*. Other inhabitants of the habitat of *L. symmetricus* occurring in less frequent numbers are *Lepisosteus oculatus*, *L. platostomus*, *Dorosoma cepedianum*, *Umbra limi*, *Cyprinus carpio*, *Ictiobus cyprinellus*, *Ictalurus natalis*, *I. nebulosus*, *Fundulus dispar*, *Aphredoderus sayanus*, *Centrarchus macropterus*, *Lepomis microlophus*, and *L. punctatus*.

REPRODUCTION

Reproductive Cycle of the Male

The genital papilla (Fig. 4) of ripe *L. symmetricus* males enlarged slightly as the spawning season approached. The testes, normally small, translucent, and elongate, became large, opaque white, and thickened.

Breeding males (Fig. 2), in contrast to non-breeding males and females (which were nearly identical in color and pattern), became very dark on the head, and the irregular vertical cross bars grew subdued. The venter from the chin and throat to the anterior rays of the anal fin became grayish black. Many small greenish flecks were present on the head and opercle, and the dark opercular spot was outlined by a silvery-cream color with a hint of suffused red. The pectoral fins were relatively dusky overall but with no definite patterns. The posterior edges of the pelvic fins were almost solid black with the remainder of the fins cream color. The dorsal fin had many light spots surrounded by dusky brown or black areas. The iris of the eye was brilliant red with a distinct black transverse bar through it.

Because of the silty darkly-stained water of Wolf Lake, no nests of *L. symmetricus* could be observed in nature, and nothing is known of territory size. However, Robison (1975:56) reported that on 23 May 1974 in a roadside pool, Saline County, Arkansas, *L. symmetricus* had recently spawned, inasmuch as "depressions in the mud and leaf litter substrate were filled with numerous eggs." Since males were observed to be highly aggressive toward females and other sunfishes are known to be territorial (Larimore 1957), it is assumed that *L. symmetricus* defends an area in nature. An aquarium-held male collected in May was seen on several occasions to form a shallow nest by rapidly swimming forward, then turning his body straight up in a vertical position

and descending, sweeping his tail vigorously back and forth until a nest depression was formed. Such nests were formed over both sand and gravel substrates. These nests were approximately 90–120 mm in diameter. It is likely that *L. symmetricus* males build shallow depressions in the mud bottom of Wolf Lake along the shallow edges close to the vegetation where egg attachment may take place. This behavior has been described for *L. cyanellus* (Hankinson 1908:210–211).

Only large males developed the breeding patterns, the slightly enlarged genital papilla, and the enlargement of the testes. Only males of at least 1+ years and 40 mm or longer appeared to be sexually mature, according to coloration and condition of the testes. The largest males probably do most or all of the spawning.

Reproductive Cycle of the Female

Generally the largest females developed the earliest mature ova and probably contributed most to the spawning effort. Females as short as or shorter than 34 mm and 1 year of age developed mature ova and were potential spawners.

Females underwent some changes in coloration associated with the breeding season. In contrast to males and non-breeding individuals, the breeding female had 9 or 10 distinct vertical bars of a dark bluish-purple color with light greenish flecks in the spaces between the bars. The cheek and opercle contained bright spots of golden green, but the fins were relatively clear and not dusky. Some females retained a diffuse ocellus in the posterior rays of the dorsal fin. As in males, the iris was bright red. Other marked morphological changes were the distended belly caused by the maturing ova and the enlargement of the genital papilla (Fig. 4). Enlargement of the papilla was noticeable only in ripe females.

Small white ova were present in females 1+ years of age and 35 mm long as early as September but were difficult to distinguish in younger and smaller females. By January and February larger yellowish ova were found in 1+-year females of 40 mm or longer. Large, coarse, maturing orange ova were present from March to May in larger and older females and in some smaller females over 34 mm and approaching 1 year of age. Just prior to spawning time, the mature ova became a translucent orange.

The largest and oldest females produced the largest number of mature ova. In 14 ripe females collected in April and May the number of ova varied from 219 to approximately 1,600 (Table 6). For these females the relationship between the number of mature ova (F) and the adjusted body weight (W) was $F = -50.94 + 210.70W$, with $r = 0.818$, and between the number of mature ova and the standard length (L) was $\log F = -2.785 + 3.383 \log L$, with $r = 0.663$.

Ovaries of postspawning females collected in June were smaller than those of females collected in April and May. They averaged slightly heavier than ovaries from females collected in March. Ovaries from females taken in July and August were small. A relative increase in ovary size was evident by late fall and continued to the spawning period the following spring (Fig. 6). For the females examined, the relationship between the weight of the ovaries divided by the adjusted body weight (Y) and the month (X), with July = 1 and May = 11, was $\log Y = 0.699 + 0.099X$, with $r = 0.782$ (Fig. 6). The proportionally largest ovaries (equaling 30.8 percent of the adjusted body weight) were found in a 51-mm, 2-year-old female collected on 27 April 1974 (UT 90.140). In the 14 females represented in Table 6, ovary-weight-to-adjusted-body-weight ratios ranged from 0.070 to 0.308 and averaged 0.107.

Table 6.—Relationship between size, age, and ovary weight of *Lepomis symmetricus* females and the number of mature ova produced. An age of 1 year = 11–13 months, 2 years = 23–25 months. Data from TCWC 3643, UT 90.140, and INHS 17583, as well as that from Wolf Lake, are included.

Standard Length in mm	Adjusted Body Weight in Grams ^a	Age in Years	Ovary Weight in Grams	Number of Mature (orange or translucent, 0.6–0.9 mm) Ova
34	1.42	1	0.10	326
34	1.49	1	0.12	219
36	1.78	1	0.13	491
37	1.65	1	0.20	368
37	2.06	1	0.18	403
38	2.32	1	0.20	330
39	2.11	1	0.21	432
40	2.43	1	0.18	417
42	2.44	1	0.26	421
43	2.75	1	0.20	374
45	3.22	1	0.33	364
45	3.34	1	0.31	378
51	4.51	2	1.39	ca 1600
52	7.57	2	0.88	ca 1400

^a Adjusted body weight is the specimen's weight after removal of the ovaries, stomach, intestine, and liver.

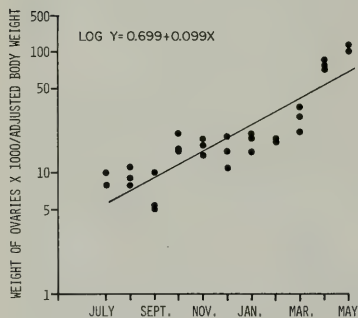


Fig. 6.—Monthly variations in ovarian weight relative to adjusted body weight of *Lepomis symmetricus*. The vertical axis is on a logarithmic scale. Ovaries from specimens collected June to April were from all age classes, but ovaries from specimens collected in May were from 2-year-old (24 months) fish.

Spawning

In Wolf Lake breeding individuals were captured as early as 24 April and as late as 30 May. Most spawning probably occurred in May when water tem-

peratures ranged from 18° to 22° C. Field observations and examination of museum specimens collected during all months of the year indicated that mid-April to early June was the typical spawning period for the species throughout its range (Table 7).

Although spawning was not observed in the study area, ripe aquarium-held individuals collected 27 May 1975 engaged in prespawning activity for 7 days at water temperatures varying from 24° to 26° C. After presumed stimulation from a recent feeding the male began to court the female by nudging her with his snout along the posterior regions of her body and continually nipping at her caudal fin. The female did not respond to these actions but the male continued to nip at her fins and nudged the female with his snout between the pelvic fins while chasing her. The female remained unresponsive. After 3 days of this behavior the male began to charge the female at rapid speeds with his opercles flared out and with the irises of his eyes more intense in color than before.

Table 7.—Collections of breeding *Lepomis symmetricus*.

Locality	Collection Date	Remarks
Wolf Lake, Union Co., Ill. (INHS 75020, 75021)	24 April–30 May 1974	Males and females in extreme breeding condition.
Pine Hills Swamp, Union Co., Ill. (INHS 17583)	27 May 1965	Female in breeding condition.
Illinois River, Tazewell Co., Ill. (INHS 75006)	2 June 1880	Females in breeding condition.
Swamp, Haywood Co., Tenn. (UT 90.140)	27 April 1974	Males and females in extreme breeding condition.
Reelfoot Lake, Lake Co., Tenn. (FMNH 80532)	8 April 1950	Males and females in breeding condition.
Roadside Ditch, Bradley Co., Ark. (UT 90.116) (HWR 74-8)	23 May 1974	Male and female in breeding condition.
Ouachita River, Union Co., Ark. (NLU 31455)	25 April 1975	Females in extreme breeding condition.
Big Hill Oil Field, Jefferson Co., Tex. (TCWC 3643)	2 May 1970	Males and females in breeding condition.
Marsh, Orleans Parish, La. (NLU 29918)	15 April 1974	Males and females in breeding condition.
Creek, Avoyelles Parish, La. (NLU 31572)	20 April 1975	Males in breeding condition.

When he approached the female, he abruptly turned himself to a vertical position (with his snout pointing upward) and gently swam around her in a close circle while fanning his tail. Similar courtship patterns were described by Larimore (1957) for *L. gulosus*. After 7 days of constant nipping, nudging, badgering, and displaying other prenuptial behavior, the male had succeeded in completely mutilating the uncooperative female's caudal fin, and on the 8th day the female was found dead. Even though an actual egg-laying session did not take place, it is evident that the nest building and prespawning behavior of *L. symmetricus* does not vary greatly from that described for other species of *Lepomis* summarized by Breder & Rosen (1966).

DEVELOPMENT AND GROWTH

Mature ova ranged in size from 0.6 to 0.9 mm in diameter, were translucent orange, and contained a single oil droplet. No data are available on incubation temperatures of eggs, the length

of time required for hatching, or the morphology of hatchlings.

The smallest *L. symmetricus* individual from the study area was 12 mm, collected 21 June 1973 (Fig. 3). At this size the nape, breast, and sides of the head were the only regions incompletely scaled, but no definite pigment pattern was present. Small melanophores outlined the scale borders on the body and some of the fin rays but were concentrated heavily on the top of the head, on the lips, and around the eye. The soft dorsal fin ocellus was just beginning to develop (Fig. 3).

A series of 43 young *L. symmetricus* from 14.0 mm to 25.0 mm was collected in the study area on 25 July 1973. At 14 mm squamation patterns were like that at 12 mm, but many more melanophores were present in the fins and they began to form patterns on the body. The ocellus was dark at this size. At 19 mm vague vertical bars had formed, and squamation was nearly complete. At 25 mm the lateralis system was developed, and the overall pigment pattern was similar to that of

adults. Squamation was complete at this stage. At a slightly larger size juveniles began to take on the form, pattern, and coloration illustrated in Fig. 3.

L. symmetricus from Wolf Lake grew at a decreasing rate (Fig. 7) and reached

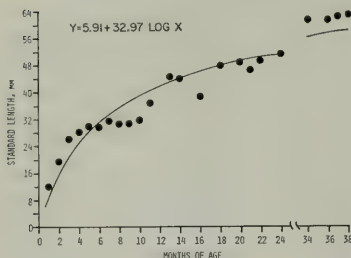


Fig. 7.—Size distribution by age of *Lepomis symmetricus* collected in Wolf Lake between 21 June 1973 and 30 May 1974. Data from 27 May 1975 and 12 December 1974 are included. Black dots represent sample means for both sexes combined. In total, 233 specimens are represented.

one-half of the first year's mean growth in approximately 10 weeks. The relationship between standard length (Y) and age in months (X) expressed for the sexes combined is $Y = 5.91 + 32.97 \log X$, with $r = 0.943$. Males grew at a slightly more rapid rate than females but were not significantly larger than females. At 13–18 months males averaged 45.9 mm and females averaged 42.7 mm ($t = 1.39$, $df = 11$). At 19–24 months males averaged 49.3 mm and females averaged 47.5 mm ($t = 1.00$, $df = 14$). The largest specimen examined from Wolf Lake was a 63.0-mm female collected 25 July 1973. In other parts of its range *L. symmetricus* is known to attain a greater length, and specimens as long as 75.5 mm have been collected (TU 148—St. Tammany Parish, Louisiana). Based on the collections examined, such large size is unusual, with most adults ranging between 55 and 60 mm.

DEMOGRAPHY

Density

The nature of the habitat of *L. symmetricus* made population density measurements difficult, since submerged logs, brush, and vegetation prevented thorough sampling of a given area. However, on two occasions approximately 5 months apart quantitative samples of *L. symmetricus* were taken in Wolf Lake by repeatedly seining a measured shallow margin of the lake until no more individuals could be collected. The number collected was translated into the number per square meter. The greatest density found for *L. symmetricus* in Wolf Lake was 0.69 sunfish per square meter (Table 8).

In the nearby LaRue-Pine Hills swamp, the density of *L. symmetricus* may approach 0.72 sunfish per square meter (Table 8) or, at best, 1 individ-

Table 8.—Number of *Lepomis symmetricus* per square meter collected in vegetated margins of Wolf Lake and LaRue-Pine Hills swamp.

Date	Number Collected	Number of <i>L. symmetricus</i> per square meter in Wolf Lake and Pine Hills
25 October 1973, Wolf Lake	9	0.313
28 March 1974, Wolf Lake	20	0.694
Mean		0.504
24 October 1973, Pine Hills	6	0.723
28 November 1973, Pine Hills	4	0.542
27 March 1974, Pine Hills	1	0.114
Mean		0.460

ual per 3 square meters in optimal habitat (Boyd *et al.* 1975). Of 31 individuals collected during 9 months at several collecting sites in Pine Hills, *L. symmetricus* made up 2.3 percent of the total sample of fishes captured.

However, more than 80 percent of the individuals were captured at one site where the habitat was judged to be optimal (Boyd *et al.* 1975). Gunning & Lewis (1955) found that *L. symmetricus* made up 5 percent of their total sample of fishes at Pine Hills.

Composition

Of the 233 *L. symmetricus* collected in Wolf Lake, 85.4 percent were up to 1 year of age, 12.4 percent were over 1 and up to 2 years of age, 0.8 percent were over 2 and up to 3 years of age, and 1.2 percent were over 3 years of age (Table 9).

Table 9.—Distribution of sexes and year classes in samples of *Lepomis symmetricus* collected in Wolf Lake between 21 June 1973 and 30 May 1974, and on 27 May 1975 and 12 December 1974.

Sex	Number by Year Class				Total
	-1	1+	2+	3+	
Males	81	16	1	..	98
Females	118	13	1	3	135
Total	199	29	2	3	233

Females predominated in the young-of-the-year (-1) age class [1.5 females to 1 male ($\chi^2 = 6.87$; $P < 0.01$)], and in the total sample ($N = 233$) the ratio was 1.4 females to 1 male ($\chi^2 = 5.97$; $P < 0.025$). Although predominating significantly in the -1 age class and in the total, females were slightly less common than males in the 1+ age class.

Survival

Relative survival values (Table 10) for each year of life were calculated for males, females, and the total sample of *L. symmetricus*, using the data in Table 9. It was assumed that each age class was collected in proportion to its relative number in the population, that the population was neither increasing nor decreasing, and that the number of fry entering the population each year was constant.

Table 10.—Relative survival of year classes of *Lepomis symmetricus* in Wolf Lake expressed as proportions of the -1 year class ($1 \times^1$) and the 1+ year class ($1 \times^2$).

Sample	Year Class	Number of Specimens	Survival	
			$1 \times^1$	$1 \times^2$
Males	-1	81	1.000	...
	1+	16	0.198	1.000
	2+	1	0.012	0.063
	3+	..	...	...
Females	-1	118	1.000	...
	1+	13	0.110	1.000
	2+	1	0.008	0.077
	3+	3	0.025	0.231
Total sample	-1	199	1.000	...
	1+	29	0.146	1.000
	2+	2	0.010	0.069
	3+	3	0.015	0.103

Because of the difficulty in collecting in Wolf Lake, the numbers of 1+ and older individuals in Tables 9 and 10 are probably lower than their actual proportion in the population.

The shapes of the survival curves for males, females, and total sample were quite similar. All showed a very low survival rate after the 1st year of life. Only three individuals 3 years or older were found. The oldest *L. symmetricus* from Wolf Lake examined was a female 3 years and 2 months old (assuming May hatching) collected 25 July 1973.

Specimens from throughout the range further confirm a 3+ -year life span for the species: INHS 17547—from LaRue-Pine Hills Ecological Area collected 16 September 1959, containing three individuals all 3 years and 4 months of age (assuming May hatching); NLU 31572—collected 20 April 1975 from a creek, Avoyelles Parish, Louisiana, containing three individuals 3 years of age. Most other species of *Lepomis* are much longer lived.

DIET

Stomach contents of 176 *L. symmetricus* from Wolf Lake were examined.

Twenty-nine of these contained no food items and eight contained green algal material. A large variety of food organisms was found (Tables 11-14). The predominant food items of the Wolf Lake population were gastropods, cladocerans, ostracods, amphipods, dragonfly naiads, chironomids, and ceratopogonids.

Small *L. symmetricus* (less than 21 mm) fed predominantly on microcrustacea, dragonfly naiads, and chironomids; large individuals (more than 40 mm) fed primarily on gastropods, dragonfly naiads, and amphipods (Tables 11 and 12). Some seasonal vari-

ation in diet (Tables 13 and 14) was evident. Gastropods were eaten in the winter and spring months. The largest percentages of most food items, including gastropods, stratiomyids, chironomids, and some microcrustacea, were eaten in the months prior to and during the spawning season, presumably reflecting an increase in consumption associated with spawning preparedness (Page 1974:17). Aquatic Hemiptera were eaten exclusively in the summer months, when they were most abundant. The presence in the diet of the exclusively terrestrial hemipteran family Fulgoridae reflects surface feeding by

Table 11.—Stomach contents of *Lepomis symmetricus* from Wolf Lake, by size class of sunfish. Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred					
	<21 mm (25)	21-30 mm (44)	31-40 mm (56)	41-50 mm (19)	51-60 mm (5)	>60 mm (5)
Gastropoda	..	..	12.5	31.6	4.0	4.0
Arachnida						
Araneae	..	2.2	1.8	..	..	..
Acarina	..	..	10.7	..	..	..
Crustacea						
Cladocera	4.0	40.9	66.1	5.2	..	..
Ostracoda	12.0	34.1	42.9	..	..	..
Copepoda	8.0	18.2	32.1	..	..	..
Amphipoda	56.0	20.0	17.9	15.8	20.0	..
Insecta						
Odonata	36.0	29.5	16.1	10.5	20.0	60.0
Coleoptera						
Helodidae	..	2.2	..	..	..	20.0
Noteridae	..	4.5	..	..	..	..
Halipilidae	..	..	10.7	..	..	..
Diptera						
Psychodidae	..	..	3.6	..	..	..
Chaoboridae	..	..	1.8	..	..	..
Tipulidae	..	..	1.8	..	..	..
Stratiomyidae	..	..	8.9	15.8	40.0	..
Ceratopogonidae	..	4.5	5.4	5.3	20.0	..
Culicidae	..	..	1.8	..	..	..
Chironomidae	52.0	4.5	25.0	..	..	..
Ephemeroptera	..	6.8	7.1	..	..	20.0
Trichoptera	..	..	5.4	5.3	..	..
Hemiptera						
Corixidae	..	9.1	8.9	21.1	..	..
Naucoridae	..	6.8	1.8	..	..	..
Fulgoridae	..	..	1.8	..	..	20.0
Pleidae	8.0	2.2	..	..	..	40.0
Mesoveliidae	..	2.2	..	..	..	..

Table 12.—Stomach contents of *Lepomis symmetricus* from Wolf Lake, by size class of sunfish. Figures in parentheses are numbers of stomachs examined.

Food Organism	Mean Number of Food Organisms Per Stomach					
	<21	21-30	31-40	41-50	51-60	>60
	mm (25)	mm (44)	mm (56)	mm (19)	mm (5)	mm (5)
Gastropoda	..	..	0.29	0.84	0.60	2.40
Arachnida						
Araneae	..	0.02	0.02	..	..	..
Acarina	..	..	0.32	..	..	..
Crustacea						
Cladocera	0.36	6.41	2.14	1.26	..	..
Ostracoda	0.48	2.57	0.07	..	..	..
Copepoda	0.12	0.91	1.25	..	..	..
Amphipoda	1.92	0.91	1.20	0.47	12.8	..
Insecta						
Odonata	0.52	0.45	0.32	0.11	0.20	1.60
Coleoptera						
Helodidae	..	0.05	..	..	..	0.20
Noteridae	..	0.07	..	..	..	..
Halipidae	..	..	0.54	..	..	..
Diptera						
Psychodidae	..	..	0.02	..	..	..
Chaoboridae	..	..	0.52	..	..	..
Tipulidae	..	..	0.04	..	..	..
Stratiomyidae	..	..	0.25	0.21	4.00	..
Ceratopogonidae	..	0.02	0.07	0.05	3.00	..
Culicidae	..	..	0.03	..	..	..
Chironomidae	0.08	0.16	0.52	..	..	..
Ephemeroptera	..	0.07	0.07	..	..	0.20
Trichoptera	..	..	0.05	0.05	..	..
Hemiptera						
Corixidae	..	0.18	0.29	0.26	..	..
Naucoridae	..	0.06	0.02	..	..	..
Fulgoridae	..	..	0.02	..	..	0.20
Pleidae	0.08	0.02	..	..	..	0.60
Mesoveliidae	..	0.02	..	..	..	..

L. symmetricus when these insects alight on the water surface.

Aquarium-held *L. symmetricus* fed in the typical *Lepomis* manner. When food was dropped into the water near them, they sucked it in or swam up near the food item and gulped it down before the food item fell to the bottom of the aquarium. Occasionally they fed off the bottom by sucking up food items. Spawning males and other individuals fed readily on dragonfly naiads, chironomids, and live and frozen earthworms. Miller & Robison (1973:184) reported aquarium-held specimens from Oklahoma feeding on "daphnia and small earthworms."

L. symmetricus has been reported to eat "dragon-fly nymphs and midge larvae" near Greenwood, Mississippi (Hildebrand & Towers 1927:134; Cook 1959:180). In 22 specimens from LaRue-Pine Hills, Illinois, the major food items were "aquatic snails, green algae, amphipods, and miscellaneous insects and insect larvae" (Gunning & Lewis 1955:556).

INTERACTION WITH OTHER ORGANISMS

Competition

L. symmetricus occurs syntopically with all other described species of *Le-*

pomis (including the introduced *L. auritus*) except *L. gibbosus*, from which it is geographically separated. Because of its preferred habitat of heavily vegetated, shallow, lentic or slow-moving water and its relative abundance there, it is doubtful that the species is geographically limited to a great degree by its several congeners.

Predation

There are no literature reports of predation on *L. symmetricus* and no evidence of such predation was found in the Wolf Lake study. As potential predators five *Micropterus salmoides*

(71.6–240.3 mm SL), four *Pomoxis nigromaculatus* (76.4–144.8 mm SL), one *P. annularis* (141.1 mm SL), five *Lepomis gulosus* (19.7–127.4 mm SL), four *L. macrochirus* (131.8–140.1 mm SL), one *Centrarchus macropterus* (82.4 mm SL), and one *Ictalurus natalis* (124.8 mm SL) were preserved and later examined for ingested *L. symmetricus*. These predators were collected from all months of the year except July and December. A number of large gar (*Lepisosteus oculatus*, *L. platostomus*) were seen during the summer and fall months but were not collected. Perhaps these large, relatively common

Table 13.—Stomach contents of *Lepomis symmetricus* from Wolf Lake by month of collection.* Figures in parentheses are numbers of stomachs examined.

Food Organism	Percent of Stomachs in Which Food Organism Occurred											
	Jan. (17)	Feb. (18)	Mar. (15)	April (9)	June (7)	July (43)	Aug. (17)	Sept. (10)	Oct. (9)	Nov. (13)	Dec. (18)	
Gastropoda	29.4	11.1	13.3	55.6	14.3	..	..	..	..	..	11.1	
Arachnida												
Araneae	..	..	..	..	..	..	..	..	..	7.7	5.6	
Acarina	..	..	26.7	22.2	..	..	..	..	..	..	..	
Crustacea												
Cladocera	17.6	44.4	20.0	33.3	..	..	76.5	90.0	77.7	61.5	16.7	
Ostracoda	..	50.0	73.3	22.2	..	11.6	52.9	..	11.1	23.1	16.7	
Copepoda	5.9	33.3	33.3	33.3	..	4.7	5.9	10.0	..	23.1	33.3	
Amphipoda	..	..	13.3	11.1	71.4	44.2	35.3	10.0	..	7.7	11.1	
Insecta												
Odonata	5.9	11.1	26.6	..	..	32.6	64.7	..	..	30.8	..	
Coleoptera												
Helodidae	..	..	..	..	..	4.7	..	..	..	..	..	
Noteridae	..	..	..	..	..	..	11.8	..	..	..	..	
Haliplidae	..	..	..	66.7	..	..	..	..	..	..	..	
Diptera												
Psychodidae	..	5.5	..	..	..	..	..	..	..	..	..	
Chaoboridae	..	5.5	..	..	..	..	..	..	..	..	..	
Tipulidae	..	..	..	..	..	..	..	..	..	7.7	..	
Stratiomyidae	29.4	11.1	..	33.3	..	..	..	..	..	..	..	
Ceratopogonidae	..	5.5	6.6	11.1	14.3	..	11.8	..	..	7.7	..	
Culicidae	..	..	..	..	..	..	5.9	..	..	..	..	
Chironomidae	5.9	22.2	..	55.6	..	7.0	5.9	20.0	..	..	11.1	
Ephemeroptera	..	..	..	..	14.3	..	..	..	..	..	38.8	
Trichoptera	..	..	..	33.3	..	..	..	..	..	..	5.6	
Hemiptera												
Corixidae	..	..	..	..	57.1	7.0	..	70.0	..	..	..	
Naucoridae	..	..	..	..	14.3	4.7	11.8	..	..	..	..	
Fulgoridae	..	..	..	..	..	4.7	5.9	..	..	..	..	
Pleidae	..	..	..	..	14.3	9.3	..	..	..	..	..	
Mesoveliidae	..	..	..	..	..	4.7	..	..	..	..	..	

* Stomach contents were not examined for May-collected specimens.

predators take some toll on the Wolf Lake population of *L. symmetricus*.

hybridization are small (Hubbs 1955: 2, 18).

Hybridization

Schwartz (1972) did not report any accounts of hybridization involving *L. symmetricus*. No evidence of hybridization was found in the Wolf Lake study area or in specimens examined from elsewhere. The small size of *L. symmetricus*, its preference for shallow, vegetated water, and its distinct breeding coloration probably preclude mis-mating of the parental species. Since there is ample habitat available in Wolf Lake and the fishes are presumably not unduly crowded, chances of

Parasitism

The Wolf Lake study population was rather heavily parasitized by plerocercoids of the cestode *Haplobothrium globuliforme*. These plerocercoids occurred in a total of 44 of 176 stomachs (25 percent) examined. From one to five plerocercoids were found in each stomach. Usually the highest numbers occurred in stomachs of the -1 year class. Specimens were found during all months of the year except May and June. The plerocercoid stage of *H. globuliforme* normally encysts in the

Table 14.—Stomach contents of *Lepomis symmetricus* from Wolf Lake by month of collection.^a Figures in parentheses are numbers of stomachs examined.

Food Organism	Mean Number of Food Organisms Per Stomach											
	Jan. (17)	Feb. (18)	Mar. (15)	April (9)	June (7)	July (43)	Aug. (17)	Sept. (10)	Oct. (9)	Nov. (13)	Dec. (18)	
Gastropoda	0.71	0.17	0.93	1.56	0.29	..	..	..	..	..	0.11	
Arachnida												
Araneae	..	..	..	..	..	..	..	..	..	0.08	0.06	
Acarina	..	..	0.93	0.44	..	..	..	..	..	..	..	
Crustacea												
Cladocera	0.06	3.61	0.93	1.67	..	..	11.35	20.00	13.22	17.23	0.72	
Ostracoda	..	7.11	10.40	0.56	..	0.44	3.00	..	0.11	0.38	0.78	
Copepoda	0.06	1.00	3.40	1.00	..	0.07	0.06	0.40	..	0.69	2.11	
Amphipoda	..	..	0.13	0.11	14.28	1.79	2.59	0.10	..	0.08	0.11	
Insecta												
Odonata	0.06	0.11	0.73	..	..	0.42	1.47	..	..	0.31	..	
Coleoptera												
Helodidae	..	..	..	..	..	0.07	..	..	..	..	..	
Noteridae	..	..	..	..	..	..	0.18	..	..	..	..	
Haliplidae	..	..	..	3.33	..	..	..	..	..	..	..	
Diptera												
Psychodidae	..	0.05	..	..	..	..	..	..	..	..	..	
Chaoboridae	..	1.61	..	..	..	..	..	..	..	..	..	
Tipulidae	..	..	..	..	..	..	..	..	..	0.15	..	
Stratiomyidae	1.41	0.11	..	1.22	..	..	..	..	..	..	..	
Ceratopogonidae	..	0.06	0.06	0.11	2.14	..	0.12	..	..	0.77	..	
Culicidae	..	..	..	..	..	..	0.12	..	..	..	..	
Chironomidae	0.41	0.39	..	1.11	..	0.09	0.06	0.40	..	..	0.22	
Ephemeroptera	..	..	..	..	0.14	..	..	..	..	..	0.39	
Trichoptera	..	..	..	0.33	..	..	..	..	..	..	0.06	
Hemiptera												
Corixidae	..	..	..	..	1.00	0.14	..	1.60	..	..	..	
Naucoridae	..	..	..	..	0.14	0.02	0.12	..	..	..	..	
Fulgoridae	..	..	..	..	..	0.02	0.14	..	..	..	..	
Pleidae	..	..	..	..	0.14	0.02	..	..	..	..	..	
Mesoveliidae	..	..	..	..	..	0.02	..	..	..	..	..	

^a Stomach contents were not examined for May-collected specimens.

liver of fishes and has been reported from a number of other fishes in both this and the adult stage (Hoffman 1967: 233). No adults were found in the study population.

One adult specimen of the acanthocephalan *Pomphorynchus bulbicollis* was found in the stomach of an *L. symmetricus* collected 24 April 1974 at Wolf Lake. Neither the cestode nor the acanthocephalan had been known to parasitize *L. symmetricus*.

Dolley (1933) reported cestodes and trematodes from "*Lepomis symmetricus* in the St. Joseph River of Michigan," but the misidentification of the host species is obvious, since *L. symmetricus* has never occurred in Michigan. Hoffman (1967), who compiled a list of fish parasites, cited for *L. symmetricus* the trematodes *Actinocleidus symmetricus*, *Cleidodiscus diversus*, and *Anchiradiscus triangularis*. Dr. Mary H. Pritchard informed me that Hoffman (1967) evidently cited as the species

name (*A. symmetricus*) that of the host instead of the parasite and that "*A. symmetricus*" does not exist. She also noted that *Cleidodiscus diversus* was described from *Lepomis cyanellus* and that its listing for *L. symmetricus* was an error in the 1964 Index-Catalogue, Trematoda and Trematode Diseases, Part 2, that was perpetuated by Hoffman (1967) and the 1969 Index-Catalogue.

One collection examined during this study from Texas (TCWC 3643) collected 2 May 1970 was heavily infested (all 32 specimens in the lot) with a monogenetic trematode, presumably *Anchoradiscus triangularis*. No external parasites were observed during the present study.

SUMMARY

The life-history information on *L. symmetricus* collected in Wolf Lake between 2 June 1973 and 27 May 1975 is summarized in Table 15.

Table 15.—Summary of life-history information on Wolf Lake *Lepomis symmetricus*.

Characteristics	Life-History Data
Principal habitat	Shallow, heavily vegetated margins of standing water
Age at reaching sexual maturity	1 year
Size at reaching sexual maturity	Females about 34 mm; males about 40 mm
Sexual dimorphism	Adult males are darker on the head and body have duskier pelvic fins and longer pelvic fins; females tend to have more distinct vertical bars
Number of mature ova in preserved females	219–1,600
Description of egg	About 0.8 mm in diameter, translucent orange
Spawning period	From mid-April to early June
Spawning habitat	Presumably in shallow water, over soft mud bottom, near plant material
Spawning site	Shallow nest depression, about 90–120 mm in diameter
Influence of sex on growth rate	Virtually none
Density	Up to 0.69 sunfish per square meter
Sex ratio among young	1.5 females : 1 male
Longevity	3+ years
Maximum size	63.0 mm standard length
Principal diet	Aquatic gastropods, insect immatures, and microcrustaceans

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